MycoKeys 124: 123–157 (2025)
DOI: 10.3897/mycokeys.124.165901

Research Article

# The subfamily Chalciporoideae (Boletaceae, Boletales) in China

Xu Zhang[1,2,3], Xin-Ni Li[1], Wei-Qing Liang[2,3], Xiao-Dong Mu[4], Ye-Fei Yu[5], Xiao-Jun Wu[2,3], Si-Yu Chen[1], Jin-Bao Pu[2,3], Nian-Kai Zeng[1]

1 *Ministry of Education Key Laboratory for Ecology of Tropical Islands, Key Laboratory of Tropical Animal and Plant Ecology of Hainan Province, College of Life Sciences, Hainan Normal University, Haikou, China*
2 *Center for Medicinal Resources Research, Zhejiang Academy of Traditional Chinese Medicine, Hangzhou, China*
3 *Zhejiang Engineering Research Center for Quality Assessment and Development of Dao-di Herbs, Hangzhou, China*
4 *Hainan Research Academy of Environmental Sciences, Haikou, China*
5 *Zhejiang Dapanshan National Natural Reserve Administration, Panan, China*

*Corresponding authors: Jin-Bao Pu (pjb0225@163.com); Nian-Kai Zeng (niankaiz@163.com)*

## Abstract

The subfamily Chalciporoideae, an early diverging lineage within Boletaceae (Boletales), is ecologically significant and economically promising. However, research on species diversity within the subfamily in China is still insufficient. In this study, detailed morphological examinations and molecular phylogenetic analyses were conducted on specimens collected from various regions in China. Three genera in Chalciporoideae, viz. *Buchwaldoboletus*, *Chalciporus*, and *Pseudophylloporus* were confirmed to be distributed in China; 16 species of the subfamily were confirmed to occur in China. Among the species recognized in China, four were newly described, viz. *Chalciporus aurantiolepidotus*, *C. brunneus*, *C. roseus*, and *Pseudophylloporus castaneus*. Two known species were redescribed, and eight other species were reviewed. Keys to the accepted species of *Buchwaldoboletus*, *Chalciporus*, and *Pseudophylloporus* were also provided, respectively.

**Key words:** Bolete, molecular phylogeny, morphology, new taxa, taxonomy

OPEN ACCESS

**Academic editor:** Yupeng Ge
**Received:** 22 July 2025
**Accepted:** 5 September 2025
**Published:** 22 October 2025

**Citation:** Zhang X, Li X-N, Liang W-Q, Mu X-D, Yu Y-F, Wu X-J, Chen S-Y, Pu J-B, Zeng N-K (2025) The subfamily Chalciporoideae (Boletaceae, Boletales) in China. MycoKeys 124: 123–157. https://doi.org/10.3897/mycokeys.124.165901

**Copyright:** © Xu Zhang et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

## Introduction

The subfamily Chalciporoideae represents one of the earliest diverging lineages within Boletaceae (Boletales). It currently includes the genera *Chalciporus* Bataille, *Buchwaldoboletus* Pilát, and the recently described *Pseudophylloporus* N.K. Zeng, H.Z. Qin, W.F. Lin & L.G. Hu (Nuhn et al. 2013; Wu et al. 2016; Qin et al. 2024; Tremble et al. 2024). Species within this subfamily are widely distributed worldwide, with particularly high diversity in tropical and subtropical regions (Desjardin et al. 2009; Nuhn et al. 2013; Raspé et al. 2016; Wu et al. 2016; Zhang et al. 2016, 2017; Xie et al. 2021; Qin et al. 2024). However, unlike most Boletaceae members that form ectomycorrhizal symbioses, the trophic modes of Chalciporoideae species are complex and not yet fully understood. Studies suggest that species within this subfamily may adopt various nutritional strategies, including ectomycorrhizal, saprotrophic, or mycoparasitic modes (Degreef and De Kesel 2008; Dickie et al. 2010, 2016; Migliorini et al. 2012). For example, *C. piperatus* (Bull.) Bataille was historically regarded as a typical ecto-

mycorrhizal fungus, but recent ecological observations, isotopic analyses, and artificial synthesis experiments indicate that it is more likely a mycoparasitic or saprotrophic fungus (Dickie and Johnston 2008; Dickie et al. 2010; Robinson 2010). Similarly, *B. lignicola* (Kallenb.) Pilát, the type species of *Buchwaldoboletus*, has been shown to function both as a mycoparasite that attacks wood-decay fungi and as a saprotroph that directly decomposes wood, exhibiting a dual trophic mode of parasitism and saprotrophy (Caiafa and Smith 2022).

The species within Chalciporoideae also exhibit significant economic and edible potential. *Chalciporus piperatus* has been widely used as a food seasoning and in dye production (Li and Song 2002; Antonio 2003; Roberts and Evans 2011). *Buchwaldoboletus xylophilus* (Petch) Both & B. Ortiz has been successfully cultivated in artificial mushroom farms, becoming the second species within the Boletales worldwide to be cultivated artificially (Yang et al. 2025). It demonstrates outstanding performance in mycelial growth rate, yield, contaminant resistance, and biological conversion efficiency, highlighting its great potential for industrialization as an emerging edible mushroom resource (Yang et al. 2025).

In recent years, multiple new species of Chalciporoideae have been described worldwide, such as *C. perezsilvae* Pérez-Moreno, Ayala-Vásquez, Mart.-Reyes & C.R. Martínez-González, *C. piedracanteadensis* Ayala-Vásquez, Pérez-Moreno & Mart.-Reyes, *C. pseudopiperatus* Klofac & Krisai, and *C. rubrostipitatus* Nanu & T.K.A. Kumar (Klofac and Krisai-Greilhuber 2020; Ayala-Vásquez et al. 2023; Nanu and Kumar 2024). Chinese researchers have played a prominent role in these efforts, contributing to the description of several new taxa, including *C. sinensis* N.K. Zeng, Chang Xu, S. Jiang & Zhi Q. Liang, *C. vulparius* N.K. Zeng, Chang Xu & Zhi Q. Liang, and *P. baishanzuensis* N.K. Zeng, H.Z. Qin, W.F. Lin & L.G. Hu (Xu et al. 2021; Qin et al. 2024). Beyond these, investigations within China have revealed additional novel taxa in this subfamily. Prior to the current study, ten species of Chalciporoideae had been recorded from China (Wu et al. 2016; Zhang et al. 2016, 2017; Xie et al. 2021; Xu et al. 2021; Mao et al. 2023; Qin et al. 2024), significantly enhancing the known diversity of Chalciporoideae. Despite these advances, the diversity of the subfamily, taxonomic relationships, and phylogenetic position of many species remain unresolved. In this study, we conducted extensive species surveys across various regions of China. Through comprehensive morphological observations and multilocus phylogenetic analyses, we clarified the species composition and phylogenetic relationships of Chalciporoideae in China. The results not only led to the discovery of new taxa, but also included the redescription of two known species and a review of seven additional species, providing a solid foundation for further investigations into the diversity and taxonomy of this subfamily.

## Materials and methods

### Morphological studies

Digital photographs and field observations were recorded on fresh basidiomata during fieldwork. Collected specimens were dried at 50–60 °C and subsequently deposited in the Hainan Biodiversity Science and Technology Museum

(**FHMU**), located in Haikou City, Hainan Province, China or the Herbarium of Medicinal Resources, Zhejiang Academy of Traditional Chinese Medicine (**ZJMR**), located in Hangzhou City, Zhejiang Province. Color descriptions follow the standard codes established by Kornerup and Wanscher (1981). Basidiomata were manually sectioned and examined microscopically after mounting in a 5% KOH solution using an Olympus CX23 optical microscope (Olympus, Tokyo, Japan). The annotation format [n/m/p] indicates the number of basidiospores (n) measured from m basidiomata belonging to p separate collections. Basidiospore measurements are reported as (a–)b–c(–d), where b–c represents the 5$^{th}$ to 95$^{th}$ percentile range of observed values, while a and d are exceptional values outside this range. The ratio of length to width is expressed as Q, with Qm representing the average Q value and its standard deviation. Descriptive terms for the size of basidiomata follow the conventions established by Bas (1969).

## Molecular procedures

For DNA extraction, small portions from the fresh basidiomata were cut, wrapped individually in paper, and sealed in bags containing silica gel to maintain dryness. Total genomic DNA was extracted from approximately 10–20 mg of dried fungal material using the Magnetic Beads Genomic DNA Extraction Kit (Magen, Guangzhou, China) according to the manufacturer's instructions. Extracted DNA samples (2 µL each) were evaluated for concentration and purity using a NanoDrop 8000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). To confirm DNA integrity, another aliquot (2 µL) was combined with an equal volume of bromophenol blue loading dye and electrophoresed on a 1% agarose gel in TAE buffer at 100 V for 20 minutes. Negative controls without DNA template were included in all extraction batches to detect potential contamination.

PCR amplification was performed on fragments of the nuclear ribosomal internal transcribed spacer (ITS), the large subunit ribosomal DNA (28S), the translation elongation factor 1-α (*TEF*1) and the RNA polymerase II second largest subunit gene (*RPB*2), employing primer pairs ITS5/ITS4 (White et al. 1990), LR0R/LR5 (Vilgalys and Hester 1990; James et al. 2006), tefF/tefR (Morehouse et al. 2003), and bRPB2-6F/bRPB2-7.1R (Matheny 2005), respectively. PCR reaction conditions were adapted from the protocols described by An et al. (2017) and Zhang et al. (2021). The 30 µL reaction mixture contained 1 µL genomic DNA template (about 20 ng), 2 µL forward and reverse primers (each at 5 pmol/µL), 15 µL of 2 × Taq PCR Master Mix, and 10 µL sterile dd$H_2O$. The PCR cycling parameters comprised an initial denaturation at 95 °C for 5 minutes, followed by 35 amplification cycles at 95 °C (30 seconds), 50 °C (30 seconds, annealing), and 72 °C (1 minute, extension). The PCR products were verified via electrophoresis on a 1% (w/v) agarose gel.

Sequencing of PCR amplicons was carried out using an ABI 3730xL DNA Analyzer by Huayu Gene (Wuhan, China). Forward and reverse chromatograms were assembled with BioEdit v7.0.9 (Hall 1999), and the resulting sequences were subsequently aligned against the NCBI nucleotide (nt) databases using the BLAST tool to identify closely related sequences. All novel sequences generated in this study have been deposited in GenBank (Table 1).

**Table 1.** Taxa, vouchers, locations, and GenBank accession numbers of DNA sequences used in this study.

| Taxon | Voucher | Locality | GenBank accession Nos. | | | | References |
|---|---|---|---|---|---|---|---|
| | | | 28S | ITS | *TEF*1 | *RPB*2 | |
| *Buchwaldoboletus lignicola* | – | – | – | MH234512 | – | – | Unpublished |
| *Buchwaldoboletus lignicola* | – | Italy | – | HM003619 | – | – | Unpublished |
| *Buchwaldoboletus lignicola* | – | Sweden | – | HM003618 | – | – | Unpublished |
| *Buchwaldoboletus lignicola* | – | United Kingdom | – | HM003617 | – | – | Unpublished |
| *Buchwaldoboletus lignicola* | 3533 | – | – | KM248950 | – | – | Unpublished |
| *Buchwaldoboletus lignicola* | KA14-0711 | South Korea | – | MH170896 | – | – | Jo et al. (2019) |
| *Buchwaldoboletus lignicola* | KA14-0907 | South Korea | – | MH170897 | – | – | Jo et al. (2019) |
| *Buchwaldoboletus lignicola* | KM157323 | – | – | GQ981493 | – | – | Bidartondo et al. (2009) |
| *Buchwaldoboletus lignicola* | HKAS76674 | Heilongjiang, NE China | KF112350 | — | KF112277 | KF112819 | Wu et al. (2016) |
| *Buchwaldoboletus lignicola* | HKAS84904 | Germany | KT990538 | — | KT990740 | KT990377 | Wu et al. (2016) |
| ***Buchwaldoboletus lignicola*** | **N.K. Zeng4946 (FHMU5579)** | **Hainan, southern China** | **PV848889** | **PV848904** | **PV871779** | **–** | **This study** |
| *Buchwaldoboletus lignicola* | Pul1 | Germany | JQ326997 | — | JQ327040 | — | Halling et al. (2012) |
| *Buchwaldoboletus lignicola* | VDKO1140 | Belgium | — | — | MH614710 | MH614756 | Vadthanarat et al. (2019) |
| *Buchwaldoboletus* sp. | JLF_X22 | USA | – | KU144820 | – | – | Frank et al. (2020) |
| ***Buchwaldoboletus xylophilus*** | **M-474 (FHMU9090)** | **Yunnan, SW China** | **PV848890** | **PV848905** | **PV871778** | **–** | **This study** |
| ***Buchwaldoboletus xylophilus*** | **ZCX-YS-01 (FHMU11666)** | **Yunnan, SW China** | **PV848891** | **PV848906** | **PV871770** | **PV877226** | **This study** |
| ***Buchwaldoboletus xylophilus*** | **ZCX-YS-02 (FHMU11667)** | **Yunnan, SW China** | **PV848892** | **PV848907** | **PV871769** | **PV877227** | **This study** |
| ***Buchwaldoboletus xylophilus*** | **ZCX-YS-03 (FHMU11668)** | **Yunnan, SW China** | **PV848893** | **PV848908** | **PV871771** | **PV877228** | **This study** |
| ***Buchwaldoboletus xylophilus*** | **ZCX-ZP-01 (FHMU11669)** | **Yunnan, SW China** | **PV848894** | **PV848909** | **PV871772** | **PV877229** | **This study** |
| ***Buchwaldoboletus xylophilus*** | **ZCX-ZP-02 (FHMU11670)** | **Yunnan, SW China** | **PV848895** | **PV848910** | **PV871773** | **PV877230** | **This study** |
| ***Buchwaldoboletus xylophilus*** | **ZCX-ZP-03 (FHMU11671)** | **Yunnan, SW China** | **PV848896** | **PV848911** | **PV871774** | **PV877231** | **This study** |
| ***Buchwaldoboletus xylophilus*** | **ZFN-CLF (FHMU11672)** | **Yunnan, SW China** | **PV848897** | **PV848912** | **PV871775** | **–** | **This study** |
| *Buchwaldoboletus xylophilus* | FHMU5930 | Yunnan, SW China | MW783417 | MW783439 | MW897330 | MW820939 | Xie et al. (2021) |
| *Buchwaldoboletus xylophilus* | FHMU5930-1 | Yunnan, SW China | MW783418 | MW783440 | MW897331 | MW820940 | Xie et al. (2021) |
| *Buchwaldoboletus xylophilus* | FHMU5931 | Yunnan, SW China | MW783419 | MW783441 | MW897332 | MW820941 | Xie et al. (2021) |
| *Buchwaldoboletus xylophilus* | FHMU5931-1 | Yunnan, SW China | MW783420 | MW783442 | MW897333 | MW820942 | Xie et al. (2021) |
| *Buchwaldoboletus xylophilus* | FHMU5932 | Yunnan, SW China | MW783421 | MW783443 | MW897334 | MW820943 | Xie et al. (2021) |
| *Buchwaldoboletus xylophilus* | FHMU5932-1 | Yunnan, SW China | MW783422 | MW783444 | MW897335 | MW820944 | Xie et al. (2021) |
| *Buchwaldoboletus xylophilus* | FHMU5933 | Yunnan, SW China | MW783423 | MW783445 | MW897336 | MW820945 | Xie et al. (2021) |
| *Buchwaldoboletus xylophilus* | FHMU5933-1 | Yunnan, SW China | MW783424 | MW783446 | MW897337 | MW820946 | Xie et al. (2021) |
| *Buchwaldoboletus xylophilus* | X.H. Deng1 (FHMU5848) | Hainan, southern China | MW783425 | — | MW897338 | MW820947 | Xie et al. (2021) |
| *Buchwaldoboletus xylophilus* | X.H. Deng2 (FHMU5849) | Hainan, southern China | MW783426 | — | MW897339 | MW820948 | Xie et al. (2021) |
| *Chalciporus* aff. *piperatus* | HKAS50214 | Yunnan, SW China | JQ928621 | – | JQ928610 | — | Hosen et al. (2012) |
| *Chalciporus africanus* | JD0517 | Cameroon | — | — | KT824029 | KT823996 | Raspé et al. (2016) |
| *Chalciporus amarellus* | DS4640-3 | Germany | KF030283 | — | KF030440 | — | Nuhn et al. (2013) |
| ***Chalciporus aurantiolepidotus*** | **N.K. Zeng7075 (FHMU7049), holotype** | **Hainan, southern China** | **PV910623** | **PV910636** | **PV891372** | **PV915955** | **This study** |
| ***Chalciporus aurantiolepidotus*** | **N.K. Zeng7076 (FHMU7056)** | **Hainan, southern China** | **PV910624** | **PV910637** | **PV891371** | **PV915956** | **This study** |

| Taxon | Voucher | Locality | GenBank accession Nos. | | | | References |
|---|---|---|---|---|---|---|---|
| | | | 28S | ITS | *TEF*1 | *RPB*2 | |
| ***Chalciporus aurantiolepidotus*** | **N.K. Zeng7352 (FHMU7472)** | **Hainan, southern China** | **PV910625** | **PV910638** | **PV891367** | **–** | **This study** |
| ***Chalciporus brunneus*** | **N.K. Zeng8522 (FHMU8246), holotype** | **Hainan, southern China** | **PV910626** | **PV910639** | **PV891368** | **PV927291** | **This study** |
| ***Chalciporus brunneus*** | **N.K. Zeng8522-1 (FHMU11617)** | **Hainan, southern China** | **PV910627** | **PV910640** | **PV891369** | **PV927292** | **This study** |
| ***Chalciporus brunneus*** | **N.K. Zeng8522-2 (FHMU11547)** | **Hainan, southern China** | **PV910628** | **PV910641** | **PV891370** | **PV927293** | **This study** |
| ***Chalciporus brunneus*** | **N.K. Zeng8522-3 (FHMU11548)** | **Hainan, southern China** | **PV910629** | **PV910642** | **PV891373** | **PV927294** | **This study** |
| *Chalciporus citrinoaurantius* | GDGM44776 | Hunan, central China | MZ157131 | OM877502 | MZ165617 | MZ165608 | Zhang et al. (2017) |
| *Chalciporus citrinoaurantius* | GDGM44480 | Hunan, central China | MZ157128 | OM877499 | MZ165614 | MZ165605 | Zhang et al. (2017) |
| *Chalciporus citrinoaurantius* | GDGM44481 | Hunan, central China | MZ157129 | OM877500 | MZ165615 | MZ165606 | Zhang et al. (2017) |
| *Chalciporus citrinoaurantius* | GDGM44717 | Hunan, central China | MZ157130 | OM877501 | MZ165616 | MZ165607 | Zhang et al. (2017) |
| *Chalciporus hainanensis* | GDGM44464 | Hainan, southern China | MZ157127 | OM877505 | MZ165612 | MZ165604 | Zhang et al. (2017) |
| *Chalciporus hainanensis* | GDGM46161 | Hainan, southern China | MZ157126 | — | MZ165613 | MZ165609 | Zhang et al. (2017) |
| *Chalciporus hainanensis* | S. Jiang81 (FHMU4573) | Hainan, southern China | MW917176 | — | MW925933 | — | Xu et al. (2021) |
| ***Chalciporus hainanensis*** | **N.K. Zeng8211 (FHMU9951)** | **Fujian, SE China** | **PV848898** | **–** | **–** | **–** | **This study** |
| *Chalciporus perezsilvae* | MEXU-HO 30438 | Mexico | OR421572 | OR421044 | — | — | Ayala-Vásquez et al. (2023) |
| *Chalciporus piedracanteadensis* | MEXU-HO 30436 | Mexico | OR421570 | OR421042 | — | — | Ayala-Vásquez et al. (2023) |
| *Chalciporus piedracanteadensis* | MEXU-HO 30437 | Mexico | OR421571 | OR421043 | — | — | Ayala-Vásquez et al. (2023) |
| *Chalciporus piperatus* | HKAS84882 | Germany | KT990562 | — | KT990758 | KT990397 | Wu et al. (2016) |
| *Chalciporus piperatus* | BJTC FM2220 | Shanxi, northern China | OR655148 | OR655148 | OR659985 | OR659936 | Mao et al. (2023) |
| *Chalciporus pseudorubinellus* | 4302 | USA | KF030284 | — | KF030441 | — | Nuhn et al. (2013) |
| *Chalciporus pseudorubinellus* | BN07 | NH, USA | KF030286 | — | — | — | Nuhn et al. (2013) |
| *Chalciporus pseudorubinellus* | DS61207 | NY, USA | KF030287 | – | KF030441 | — | Nuhn et al. (2013) |
| *Chalciporus radiatus* | GDGM43285 | Hunan, central China | KP871800 | KP871804 | MZ165610 | — | Zhang et al. (2016); Zhang et al. (2017) |
| *Chalciporus radiatus* | GDGM43305 | Guangdong, southern China | KP871802 | — | — | — | Zhang et al. (2016) |
| *Chalciporus radiatus* | GDGM50080 | Hunan, central China | KP871801 | KP871806 | MZ165611 | — | Zhang et al. (2016); Zhang et al. (2017) |
| ***Chalciporus radiatus*** | **N.K. Zeng10292 (FHMU8509)** | **Zhejiang, eastern China** | **PV848899** | **PV848913** | **PV871776** | **PV877232** | **This study** |
| ***Chalciporus radiatus*** | **N.K. Zeng10296 (FHMU8989)** | **Zhejiang, eastern China** | **PV848900** | **–** | **PV871777** | **PV877233** | **This study** |
| *Chalciporus radiatus* | N.K. Zeng1379 (FHMU930) | Fujian, SE China | MH879710 | — | MH879738 | — | Chai et al. (2019) |
| *Chalciporus radiatus* | N.K. Zeng1414 (FHMU959) | Fujian, SE China | MH879711 | — | MH879739 | — | Chai et al. (2019) |
| *Chalciporus radiatus* | N.K. Zeng1808 (FHMU 2494) | Hainan, southern China | — | — | MH879737 | — | Chai et al. (2019) |
| ***Chalciporus roseus*** | **N.K. Zeng8516 (FHMU7888), holotype** | **Hainan, southern China** | **PV910630** | **PV910643** | **PV891611** | **–** | **This study** |
| ***Chalciporus roseus*** | **N.K. Zeng8516-1 (FHMU11614)** | **Hainan, southern China** | **PV910631** | **PV910644** | **PV891612** | **–** | **This study** |

| Taxon | Voucher | Locality | GenBank accession Nos. | | | | References |
|---|---|---|---|---|---|---|---|
| | | | 28S | ITS | *TEF*1 | *RPB*2 | |
| ***Chalciporus roseus*** | **N.K. Zeng8516-2 (FHMU11615)** | **Hainan, southern China** | **PV910632** | **PV910645** | **PV915952** | **–** | **This study** |
| *Chalciporus rubinelloides* | HKAS57362 | Yunnan, SW China | KT990563 | — | KT990759 | KT990398 | Wu et al. (2016) |
| *Chalciporus rubinelloides* | HKAS58728 | Yunnan, SW China | KT990564 | — | KT990760 | KT990399 | Wu et al. (2016) |
| *Chalciporus rubinelloides* | HKAS74952 | Yunnan, SW China | KT990565 | — | KT990761 | KT990400 | Wu et al. (2016) |
| *Chalciporus rubinelloides* | HKAS75034 | Yunnan, SW China | KT990566 | — | — | — | Wu et al. (2016) |
| *Chalciporus rubinellus* | 191/81 | USA | EU685106 | — | — | — | Desjardin et al. (2009) |
| *Chalciporus rubrostipitatus* | ZGCSN153 | India | OQ193026 | OQ225690 | — | OQ993343 | Nanu and Kumar (2024) |
| *Chalciporus rubrostipitatus* | ZGCSN160 | India | — | OQ231504 | — | — | Nanu and Kumar (2024) |
| *Chalciporus sinensis* | N.K. Zeng4478 (FHMU4701) | Hainan, southern China | MW917171 | — | MW925928 | MW925934 | Xu et al. (2021) |
| *Chalciporus sinensis* | N.K. Zeng4479 (FHMU4691) | Hainan, southern China | MW917172 | — | MW925929 | MW925935 | Xu et al. (2021) |
| *Chalciporus* sp. | GDGM43250 | Guangdong, southern China | MZ157125 | — | — | — | Zhang et al. (2017) |
| *Chalciporus* sp. | HKAS53400 | Hunan, central China | KF112352 | — | KF112279 | KF112821 | Wu et al. (2023) |
| *Chalciporus* sp. | OR0363 | Thailand | — | — | MH645594 | MH645602 | Vadthanarat et al. (2019) |
| *Chalciporus* sp. | X.T. Zhu134 (FHMU2721) | Yunnan, SW China | MW917175 | — | MW925932 | — | Xu et al. (2021) |
| *Chalciporus vulparius* | N.K. Zeng4978 (FHMU5554) | Hainan, southern China | MW917173 | — | MW925930 | MW925936 | Xu et al. (2021) |
| *Chalciporus vulparius* | N.K. Zeng4979 (FHMU5560) | Hainan, southern China | MW917174 | — | MW925931 | MW925937 | Xu et al. (2021) |
| *Paxillus obscurosporus* | Po1 | Germany | AY177256 | – | KF030442 | – | Nuhn et al. (2013); Wu et al. (2016) |
| *Paxillus vernalis* | AFTOL-ID 715 | – | AY645059 | DQ647827 | DQ457629 | – | Binder and Hibbett (2006); Matheny et al. (2006) |
| *Pseudophylloporus baishanzuensis* | N.K. Zeng7702 (FHMU7694) | Zhejiang, eastern China | PQ330210 | – | PQ330110 | PQ330114 | Qin et al. (2024) |
| *Pseudophylloporus baishanzuensis* | N.K. Zeng7703 (FHMU7695) | Zhejiang, eastern China | PQ330211 | – | PQ330111 | PQ330115 | Qin et al. (2024) |
| *Pseudophylloporus baishanzuensis* | N.K. Zeng7705 (FHMU7696) | Zhejiang, eastern China | PQ330212 | – | PQ330112 | PQ330116 | Qin et al. (2024) |
| *Pseudophylloporus baishanzuensis* | N.K. Zeng7746 (FHMU7697) | Zhejiang, eastern China | PQ330213 | – | PQ330113 | PQ330117 | Qin et al. (2024) |
| ***Pseudophylloporus castaneus*** | **FC330727230331 (ZJMR330727230331), holotype** | **Zhejiang, eastern China** | **PV910633** | **PV910646** | **–** | **–** | **This study** |
| ***Pseudophylloporus castaneus*** | **FC330727230331-1 (FHMU11549)** | **Zhejiang, eastern China** | **PV910634** | **PV910647** | **PV915953** | **–** | **This study** |
| ***Pseudophylloporus castaneus*** | **FC330727230331-2 (FHMU11550)** | **Zhejiang, eastern China** | **PV910635** | **PV910648** | **PV915954** | **–** | **This study** |

GenBank numbers in bold indicate the newly generated sequences; SE, Southeastern; SW, Southwest; NE, Northeast.

## Dataset assembly

A total of 85 novel DNA sequences (including 25 for 28S, 23 for ITS, 23 for *TEF*1, and 14 for *RPB*2) were obtained from 25 collections. These sequences, along with reference sequences retrieved from GenBank and previously published literature (Table 1), were combined to construct a concatenated dataset

comprising the 28S, ITS, *TEF*1, and *RPB*2 gene regions. Reference sequences were selected based on the following criteria: (i) preference for sequences derived from type material when available; (ii) inclusion of high-quality sequences with multiple gene fragments from published studies; and (iii) ensuring broad taxonomic and geographic representation of Chalciporoideae. Following Wu et al. (2016), *Paxillus vernalis* Watling and *P. obscurosporus* C. Hahn were selected as outgroup taxa. To detect potential phylogenetic conflicts among the four gene regions within the combined dataset, single-gene analyses were performed separately for the 28S, ITS, *TEF*1, and *RPB*2 sequences. Results indicated no significant incongruence among these gene trees. Subsequently, individual gene sequences were aligned using MUSCLE v3.6 (Edgar 2004) and manually refined using BioEdit software (Hall 1999). Finally, aligned sequences were concatenated utilizing Phyutility version 2.2 (Smith and Dunn 2008) for downstream phylogenetic analysis.

### Phylogenetic analyses

For the phylogenetic reconstruction based on the concatenated dataset (28S + ITS + *TEF*1 + *RPB*2), both Maximum Likelihood (ML) and Bayesian Inference (BI) methodologies were utilized. ML analyses and associated bootstrap tests were executed using RAxML v7.2.6 (Stamatakis 2006). The GTRGAMMA substitution model was selected for ML analyses, while all other settings remained at default values. Support values were estimated via nonparametric bootstrap analysis with 1000 replicates. Bayesian analyses employed Markov Chain Monte Carlo (MCMC) sampling using MrBayes v3.1 (Huelsenbeck and Ronquist 2005; Miller et al. 2011). Two parallel MCMC runs, each comprising four simultaneous chains, were carried out. Trees were sampled every 100 generations. Parameter settings followed default options, guided by MrModeltest v2.3 recommendations (Nylander 2004). The initial 25% of sampled trees were excluded as burn-in, and the remaining trees were used to generate a majority-rule consensus tree, with posterior probability (PP) values calculated accordingly.

## Results

### Molecular data

The dataset, combining 28S, ITS, *TEF*1, and *RPB*2, included 95 sequences with 2141 nucleotide positions (28S: 652 bp; ITS: 500 bp; *TEF*1: 373 bp; *RPB*2: 616 bp). Of these, 588 sites were variable and 533 were parsimony-informative. Bayesian analyses for the multi-gene dataset were run for 30 million generations, reaching convergence with an average standard deviation of split frequencies at 0.000499. The optimal nucleotide substitution models for each gene partition were identified as SYM + G for 28S, ITS, *TEF*1, and *RPB*2. The Bayesian analyses produced topologies identical to those of the ML analysis, with slight differences in statistical support (Fig. 1). The collections of Chalciporoideae from China were grouped into 16 independent species-level lineages (Fig. 1).

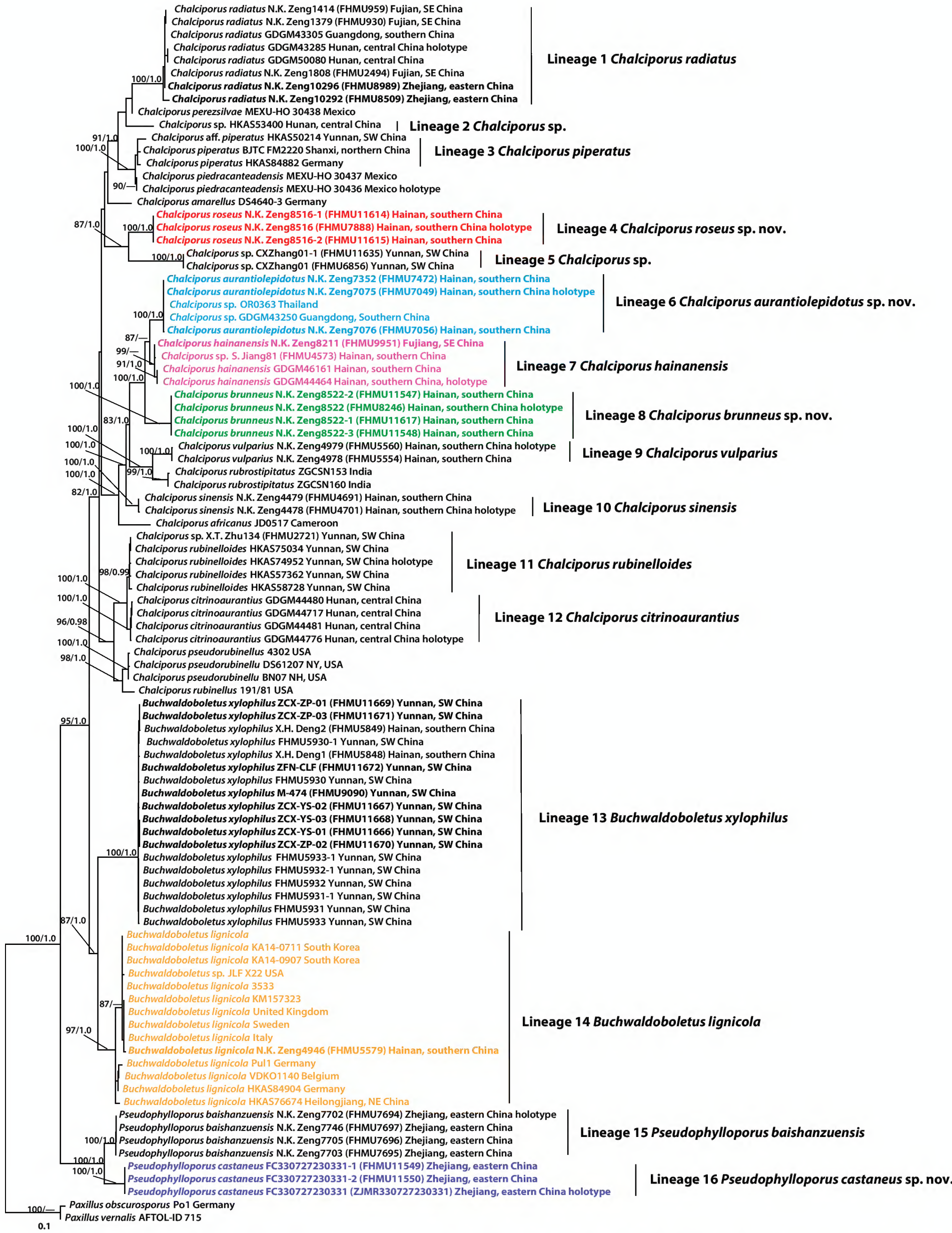
Chalciporus radiatus N.K. Zeng1414 (FHMU959) Fujian, SE China
Chalciporus radiatus N.K. Zeng1379 (FHMU930) Fujian, SE China
Chalciporus radiatus GDGM43305 Guangdong, southern China
Chalciporus radiatus GDGM43285 Hunan, central China holotype
Chalciporus radiatus GDGM50080 Hunan, central China
Chalciporus radiatus N.K. Zeng1808 (FHMU2494) Fujian, SE China
Chalciporus radiatus N.K. Zeng10296 (FHMU8989) Zhejiang, eastern China
Chalciporus radiatus N.K. Zeng10292 (FHMU8509) Zhejiang, eastern China
Lineage 1 Chalciporus radiatus
Chalciporus perezsilvae MEXU-HO 30438 Mexico
Chalciporus sp. HKAS53400 Hunan, central China
Lineage 2 Chalciporus sp.
Chalciporus aff. piperatus HKAS50214 Yunnan, SW China
Chalciporus piperatus BJTC FM2220 Shanxi, northern China
Chalciporus piperatus HKAS84882 Germany
Lineage 3 Chalciporus piperatus
Chalciporus piedracanteadensis MEXU-HO 30437 Mexico
Chalciporus piedracanteadensis MEXU-HO 30436 Mexico holotype
Chalciporus amarellus DS4640-3 Germany
Chalciporus roseus N.K. Zeng8516-1 (FHMU11614) Hainan, southern China
Chalciporus roseus N.K. Zeng8516 (FHMU7888) Hainan, southern China holotype
Chalciporus roseus N.K. Zeng8516-2 (FHMU11615) Hainan, southern China
Lineage 4 Chalciporus roseus sp. nov.
Chalciporus sp. CXZhang01-1 (FHMU11635) Yunnan, SW China
Chalciporus sp. CXZhang01 (FHMU6856) Yunnan, SW China
Lineage 5 Chalciporus sp.
Chalciporus aurantiolepidotus N.K. Zeng7352 (FHMU7472) Hainan, southern China
Chalciporus aurantiolepidotus N.K. Zeng7075 (FHMU7049) Hainan, southern China holotype
Chalciporus sp. OR0363 Thailand
Chalciporus sp. GDGM43250 Guangdong, Southern China
Chalciporus aurantiolepidotus N.K. Zeng7076 (FHMU7056) Hainan, southern China
Lineage 6 Chalciporus aurantiolepidotus sp. nov.
Chalciporus hainanensis N.K. Zeng8211 (FHMU9951) Fujiang, SE China
Chalciporus sp. S. Jiang81 (FHMU4573) Hainan, southern China
Chalciporus hainanensis GDGM46161 Hainan, southern China
Chalciporus hainanensis GDGM44464 Hainan, southern China, holotype
Lineage 7 Chalciporus hainanensis
Chalciporus brunneus N.K. Zeng8522-2 (FHMU11547) Hainan, southern China
Chalciporus brunneus N.K. Zeng8522 (FHMU8246) Hainan, southern China holotype
Chalciporus brunneus N.K. Zeng8522-1 (FHMU11617) Hainan, southern China
Chalciporus brunneus N.K. Zeng8522-3 (FHMU11548) Hainan, southern China
Lineage 8 Chalciporus brunneus sp. nov.
Chalciporus vulparius N.K. Zeng4979 (FHMU5560) Hainan, southern China holotype
Chalciporus vulparius N.K. Zeng4978 (FHMU5554) Hainan, southern China
Lineage 9 Chalciporus vulparius
Chalciporus rubrostipitatus ZGCSN153 India
Chalciporus rubrostipitatus ZGCSN160 India
Chalciporus sinensis N.K. Zeng4479 (FHMU4691) Hainan, southern China
Chalciporus sinensis N.K. Zeng4478 (FHMU4701) Hainan, southern China holotype
Lineage 10 Chalciporus sinensis
Chalciporus africanus JD0517 Cameroon
Chalciporus sp. X.T. Zhu134 (FHMU2721) Yunnan, SW China
Chalciporus rubinelloides HKAS75034 Yunnan, SW China
Chalciporus rubinelloides HKAS74952 Yunnan, SW China holotype
Chalciporus rubinelloides HKAS57362 Yunnan, SW China
Chalciporus rubinelloides HKAS58728 Yunnan, SW China
Lineage 11 Chalciporus rubinelloides
Chalciporus citrinoaurantius GDGM44480 Hunan, central China
Chalciporus citrinoaurantius GDGM44717 Hunan, central China
Chalciporus citrinoaurantius GDGM44481 Hunan, central China
Chalciporus citrinoaurantius GDGM44776 Hunan, central China holotype
Lineage 12 Chalciporus citrinoaurantius
Chalciporus pseudorubinellus 4302 USA
Chalciporus pseudorubinellu DS61207 NY, USA
Chalciporus pseudorubinellu BN07 NH, USA
Chalciporus rubinellus 191/81 USA
Buchwaldoboletus xylophilus ZCX-ZP-01 (FHMU11669) Yunnan, SW China
Buchwaldoboletus xylophilus ZCX-ZP-03 (FHMU11671) Yunnan, SW China
Buchwaldoboletus xylophilus X.H. Deng2 (FHMU5849) Hainan, southern China
Buchwaldoboletus xylophilus FHMU5930-1 Yunnan, SW China
Buchwaldoboletus xylophilus X.H. Deng1 (FHMU5848) Hainan, southern China
Buchwaldoboletus xylophilus ZFN-CLF (FHMU11672) Yunnan, SW China
Buchwaldoboletus xylophilus FHMU5930 Yunnan, SW China
Buchwaldoboletus xylophilus M-474 (FHMU9090) Yunnan, SW China
Buchwaldoboletus xylophilus ZCX-YS-02 (FHMU11667) Yunnan, SW China
Buchwaldoboletus xylophilus ZCX-YS-03 (FHMU11668) Yunnan, SW China
Buchwaldoboletus xylophilus ZCX-YS-01 (FHMU11666) Yunnan, SW China
Buchwaldoboletus xylophilus ZCX-ZP-02 (FHMU11670) Yunnan, SW China
Buchwaldoboletus xylophilus FHMU5933-1 Yunnan, SW China
Buchwaldoboletus xylophilus FHMU5932-1 Yunnan, SW China
Buchwaldoboletus xylophilus FHMU5932 Yunnan, SW China
Buchwaldoboletus xylophilus FHMU5931-1 Yunnan, SW China
Buchwaldoboletus xylophilus FHMU5931 Yunnan, SW China
Buchwaldoboletus xylophilus FHMU5933 Yunnan, SW China
Lineage 13 Buchwaldoboletus xylophilus
Buchwaldoboletus lignicola
Buchwaldoboletus lignicola KA14-0711 South Korea
Buchwaldoboletus lignicola KA14-0907 South Korea
Buchwaldoboletus sp. JLF X22 USA
Buchwaldoboletus lignicola 3533
Buchwaldoboletus lignicola KM157323
Buchwaldoboletus lignicola United Kingdom
Buchwaldoboletus lignicola Sweden
Buchwaldoboletus lignicola Italy
Buchwaldoboletus lignicola N.K. Zeng4946 (FHMU5579) Hainan, southern China
Buchwaldoboletus lignicola Pul1 Germany
Buchwaldoboletus lignicola VDKO1140 Belgium
Buchwaldoboletus lignicola HKAS84904 Germany
Buchwaldoboletus lignicola HKAS76674 Heilongjiang, NE China
Lineage 14 Buchwaldoboletus lignicola
Pseudophylloporus baishanzuensis N.K. Zeng7702 (FHMU7694) Zhejiang, eastern China holotype
Pseudophylloporus baishanzuensis N.K. Zeng7746 (FHMU7697) Zhejiang, eastern China
Pseudophylloporus baishanzuensis N.K. Zeng7705 (FHMU7696) Zhejiang, eastern China
Pseudophylloporus baishanzuensis N.K. Zeng7703 (FHMU7695) Zhejiang, eastern China
Lineage 15 Pseudophylloporus baishanzuensis
Pseudophylloporus castaneus FC330727230331-1 (FHMU11549) Zhejiang, eastern China
Pseudophylloporus castaneus FC330727230331-2 (FHMU11550) Zhejiang, eastern China
Pseudophylloporus castaneus FC330727230331 (ZJMR330727230331) Zhejiang, eastern China holotype
Lineage 16 Pseudophylloporus castaneus sp. nov.
Paxillus obscurosporus Po1 Germany
Paxillus vernalis AFTOL-ID 715
0.1

**Figure 1.** Phylogram of Chalciporoideae inferred from multilocus (rDNA 28S, ITS, *TEF*1, and *RPB*2) dataset using RAxML. RAxML bootstrap percentages (BS ≥ 70%) and Bayesian posterior probabilities (PP ≥ 0.95) are indicated above or below the branches as BS/PP. Note. SE = southeastern China; SW = southwestern China; NE = northeastern China.

## Taxonomy

### Key to genera of Chalciporoideae

1 Hymenophore lamellate, clamp connections present....***Pseudophylloporus***
– Hymenophore poroid, clamp connections absent .....**2**
2 Pileus surface tomentose or pulverulent, yellow to brownish; pore surface initially light yellow to ochraceous yelow..... ***Buchwaldoboletus***
– Pileus surface glabrous to obscurely subtomentose, pinkish-red to reddish-brown; pore surface pinkish red to reddish brown, yellow....***Chalciporus***

### *Buchwaldoboletus* Pilát, Friesia 9 (1–2): 217, 1969

*Buchwaldoboletus*, typified by *B. lignicola*, is mainly characterized by its saprotrophic and lignicolous lifestyle, a dry, pulverulent to tomentose pileus, yellow to golden hymenophore changing blue when injured, and an interwoven pileipellis (Pilát 1969; Ortiz-Santana and Both 2011; Wu et al. 2016). Until now, two species, viz. *B. lignicola* and *B. xylophilus* have been confirmed to occur in China (Wu et al. 2016; Xie et al. 2021).

### *Buchwaldoboletus lignicola* (Kallenb.) Pilát, Friesia. 9 (1–2): 217, 1969

MycoBank No: 327206
Figs 2a, b, 3

*Boletus lignicola* Kallenb., Die Pilze Mitteleuropas, Band 1, Die Röhrlinge (Boletaceae): 57, 1929.
*Xerocomus lignicola* (Kallenb.) Singer, Annales Mycologici 40: 43, 1942.
*Phlebopus lignicola* (Kallenb.) M.M. Moser ex Groves, Mycologia 54: 320, 1962.
*Pulveroboletus lignicola* (Kallenb.) E.A. Dick & Snell, Mycologia 57: 451, 1965.
*Gyrodon lignicola* (Kallenb.) Heinem., Bulletin du Jardin Botanique de l'État à Bruxelles 21: 238, 1951.

**Description.** ***Basidiomata*** small-sized. Pileus 3–4 cm in diameter, subhemispherical to convex; surface dry, finely tomentose, orangish-yellow to golden-yellow (4A6–5A7); context 0.4–0.6 cm in thickness in the center of the pileus, white (1A1) to yellowish (1A2), unchanging in color when bruised. ***Hymenophore*** poroid, slightly decurrent; pores angular to roundish, yellow, changing greenish-blue when bruised; tubes 0.1–0.3 cm long, yellow, changing greenish-blue when bruised. ***Stipe*** 3–5 × 1–2 cm, central, solid, subcylindrical, surface tomentose, upper part pale yellow to yellow (3A4–3A5), lower part orangish-brown to ochre (5C5–6C6); context white (1A1) to yellowish (1A2), unchanging in color when bruised; basal mycelium white. ***Odor*** indistinct. ***Taste*** mild.

***Basidiospores*** [40/2/1] (6)6.5–9 × (3)3.5–4 µm, Q= (1.5)1.75–3.0, Qm = 2.30 ± 0.32, yellowish brown in KOH, elongated to cylindrical, slightly thick-walled (0.8–1 µm), smooth under the light microscope. ***Basidia*** 14–29 × 5–8 µm, clavate, slightly thick-walled (up to 1 µm), 4-spored, hyaline to pale yellow in

**Figure 2.** Basidiomata of fungi in the subfamily Chalciporoideae **a, b.** *Buchwaldoboletus lignicola* (FHMU5579); **c–e.** *Chalciporus aurantiolepidotus* (**c, e** FHMU7049, holotype; **d** FHMU7472); **f–h.** *C. brunneus* (FHMU8246, holotype); **i.** *C. hainanensis* (FHMU9951); **j–l.** *C. roseus* (FHMU7888, holotype); **m–o.** *Pseudophylloporus castaneus* (ZJMR330727230331, holotype). Scale bars: 1 cm. **a–l.** photos by N.K. Zeng; **m–o.** photos by J.B. Pu.

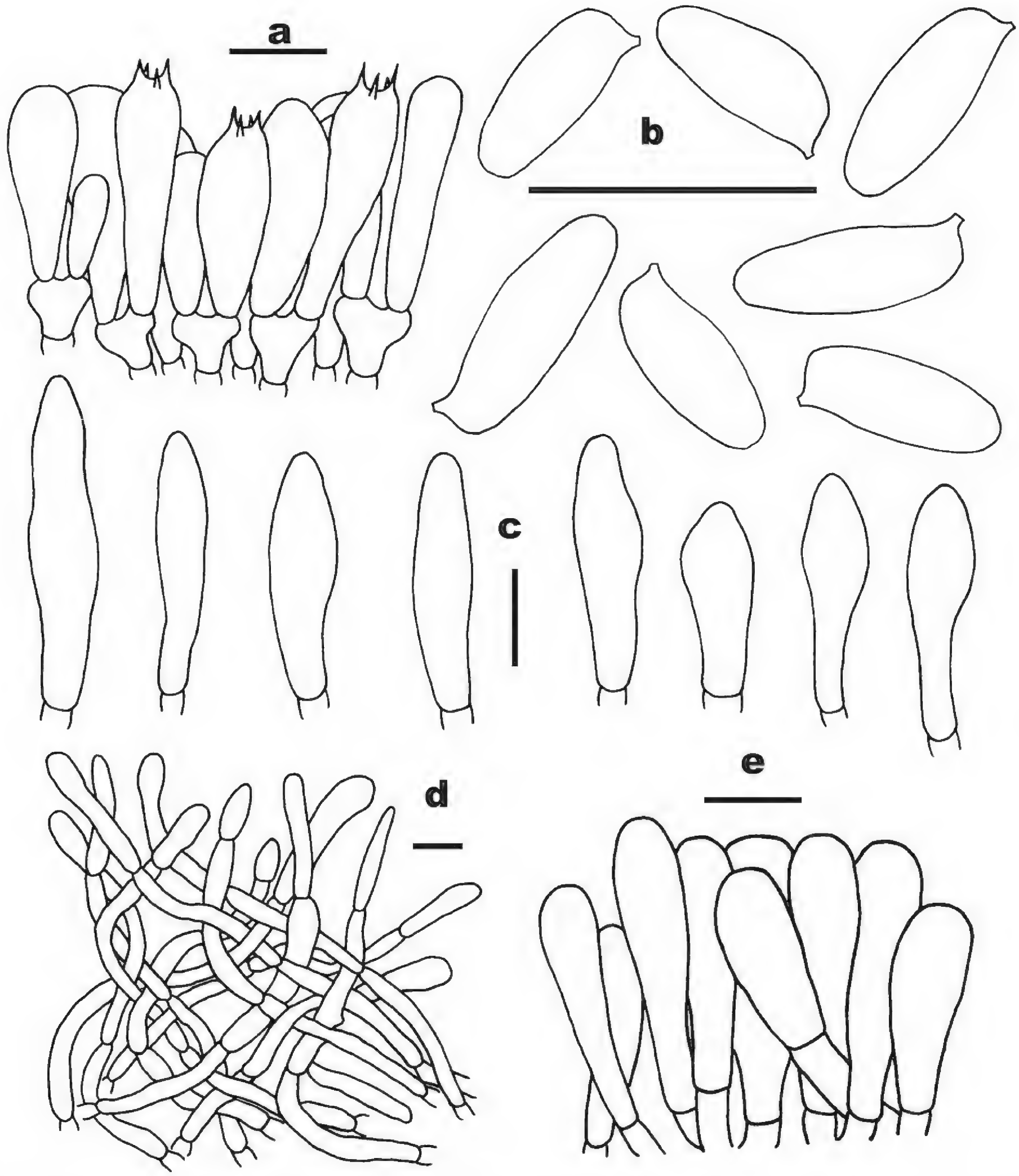


**Figure 3.** Microscopic features of *Buchwaldoboletus lignicola* (FHMU5579). **a.** Basidia; **b.** Basidiospores; **c.** Cystidia; **d.** Pileipellis; **e.** Stipitipellis. Scale bars: 10 μm. Drawings by X.N. Li.

KOH; sterigmata 2–5 μm in length. ***Cystidia*** 20–35 × 5–7 μm, fusiform or subfusiform, slightly thick-walled (up to 1 μm), pale yellow in KOH. ***Hymenophoral trama*** boletoid, colorless to yellowish in KOH, thin- to slightly thick-walled (up to 0.5 μm), 6–12 μm wide. ***Pileipellis*** an intricate trichoderm 400–550 μm in thickness, composed of hyaline to pale yellow in KOH, slightly thick-walled (up to 1 μm) hyphae; terminal cells 9–37 × 3–7 μm, clavate to subcylindrical or cystidioid. ***Pileus trama*** made up of hyphae 2–9 μm in diameter, thick-walled (up to 1.5 μm), yellow in KOH. ***Stipitipellis*** a trichoderm-like structure 160–200 μm thick, composed of pale yellow in KOH, thin-walled hyphae; terminal cells 18–

27× 5–8 µm, clavate or subcylindrical. ***Stipe trama*** composed of parallel hyphae 2–16 µm in diameter, cylindrical, thin-walled, yellow in KOH. ***Clamp connections*** absent in all tissues.

**Habitat.** Solitary on the ground in broadleaf forest.

**Known distribution.** Southern (Hainan Province) and northeastern China (Heilongjiang Province); Europe, North America, Nepal, Korea, and Indonesia (Kallenbach 1929; Aryal and Budathoki 2013; Wu et al. 2016; Venturella 2017; Jo et al. 2019; Putra et al. 2025).

**Material examined.** China • Hainan Province, Changjiang County, Bawangling of Hainan Tropical Rainforest National Park, elev. 650 m, 2 September 2020, N.K. Zeng4946 (FHMU5579).

**Notes.** *Buchwaldoboletus lignicola* was originally described from Germany by Kallenbach (1929). In China, it was reported from the northeastern region of the country (Wu et al. 2016). In the present study, it was also found to be distributed in Hainan Province, southern China. The species is characterized by a dry, tomentose, orangish-yellow to golden-yellow pileus, a yellow hymenophore bruising greenish-blue, and an intricate trichodermal pileipellis. Based on our specimen, a diagnostic feature described by Wu et al. (2016), viz., doliform to subglobose cells often forming chains in the pileipellis, was not observed. Such cellular morphology has not been reported in other recent descriptions of *B. lignicola*, including specimens from Korea (Jo et al. 2019).

***Buchwaldoboletus xylophilus*** **(Petch) Both & B. Ortiz, Bull. Buffalo Soc. Nat. Sci. 40: 3, 2011**

MycoBank No: 545884

*Boletus xylophilus* Petch, Ann. Roy. Bot. Gard. Peradeniya 7 (4): 283, 1922.

*Gyrodon xylophilus* (Petch) Heinem. & Rammeloo, Bull. Jard. Bot. Natl. Belg. 53 (1–2): 295, 1983.

*Pulveroboletus xylophilus* (Petch) Singer, in Singer, Araujo & Ivory, Beih. Nova Hedwigia 77: 98, 1983.

**Known distribution.** Southwestern (Yunnan Province) and southern China (Hainan Province and Hong Kong); Sri Lanka, Malaysia, India, and the Philippines (Pegler 1986; Corner 1972; Ortiz-Santana and Both 2011; Xie et al. 2021; Nanu and Kumar 2022).

**Holotype.** Petch 5812 (K) (Sri Lanka) (non vidi).

**Materials examined.** China • Yunnan Province, Xishuangbanna, cultivated at the Yunnan Institute of Tropical Crops, December 2023, M-474 (FHMU9090); • same location and date, ZCX-YS-01 (FHMU11666); • same location and date, ZCX-YS-02 (FHMU11667); • same location and date, ZCX-YS-03 (FHMU11668); • same location and date, ZCX-ZP-01 (FHMU11669); • same location and date, ZCX-ZP-02 (FHMU11670); • same location and date, ZCX-ZP-03 (FHMU11671); • same location and date, ZFN-CLF (FHMU11672).

**Notes.** *Buchwaldoboletus xylophilus* was originally described from Sri Lanka by Petch (1922). It was also reported from southwestern and southern China (Xie et al. 2021; Mao et al. 2023). Illustrations and a full description of the species have been provided by Ortiz-Santana and Both 2011 and Xie et al. (2021).

## Key to accepted *Buchwaldoboletus* species in China

1 Pileus orangish-yellow; context unchanging in color when bruised; basidiospores elongated, measuring 6.5–9 × 3.5–4 µm, Qm = 2.30 ± 0.32..... ..... ***B. lignicola***

– Pileus yellowish-brown; context turning blue in color when bruised; basidiospores subglobose to short-ellipsoid, measuring 4.5–6 × 3–4.5 µm, Qm = 1.38 ± 0.23 .....***B. xylophilus***

### *Chalciporus* Bataille, Bull. Soc. Hist. Nat. Doubs 15: 39, 1908

*Chalciporus*, typified by *C. piperatus*, was originally established to accommodate species with a small basidioma, a reddish hymenophore, and smooth basidiospores (Moreno and García-Bona 1976; Pegler and Young 1981; Pegler 1983; Baroni and Both 1991; Gómez 1996; Halling et al. 2004; Klofac and Krisai-Greilhuber 2006). Besides the three new *Chalciporus* species revealed in the present study, seven species of the genus have been confirmed to occur in China (Wu et al. 2016; Zhang et al. 2016, 2017; Deng et al. 2018; Chai et al. 2019; Xu et al. 2021; Mao et al. 2023).

### *Chalciporus aurantiolepidotus* N.K. Zeng & X. Zhang, sp. nov.

MycoBank No: 860039

Figs 2c–e, 4

**Etymology.** Latin "*aurantiolepidotus*", referring to the orange squamules on the pileal surface.

**Holotype.** CHINA • Hainan Province, Changjiang County, Bawangling of Hainan Tropical Rainforest National Park, alt. 650 m, 19.1°N, 109.2°E, 8 May 2022, N.K. Zeng7075 (FHMU7049).

**Diagnosis.** Differs from closest species of *Chalciporus* by a very small basidioma, a dry pileus covered with orange to reddish squamules, a reddish-orange to reddish hymenophore, and a trichodermal pileipellis.

**Description.** ***Basidiomata*** very small-sized. ***Pileus*** 2–2.5 cm in diameter, subhemispherical to convex when young, plano-convex to applanate when mature, margin occasionally upturned; surface dry, covered with orange (6B4) to reddish (6B3) squamules; context 0.2–0.3 cm in thickness in the center of the pileus, white (1A1), unchanging in color when bruised. ***Hymenophore*** poroid, slightly decurrent; pores angular, 0.1–0.25 cm wide, reddish-orange (7A4) to reddish (8A5), unchanging in color when bruised; tubes 0.2–0.3 cm long, reddish (8A5), unchanging in color when bruised. ***Stipe*** 1.6–1.7 × 0.3 cm, central, solid, subcylindrical; surface pale brown, with distinctly longitudinal striations; context white (1A1), unchanging in color when bruised; basal mycelium white. ***Odor*** indistinct. ***Taste*** mild.

***Basidiospores*** [60/8/3] (8)8.5–11(12) × 4–5 µm, Q= (1.6)1.7–2.5(3.0), $Q_m$ = 2.22 ± 0.28, yellowish-brown in KOH, elongated to cylindrical, slightly thick-walled (0.8–1 µm), smooth under the light microscope. ***Basidia*** 18–30 × 8–12 µm, clavate, slightly thick-walled (up to 1 µm), 4-spored, colorless to pale yellow in KOH;

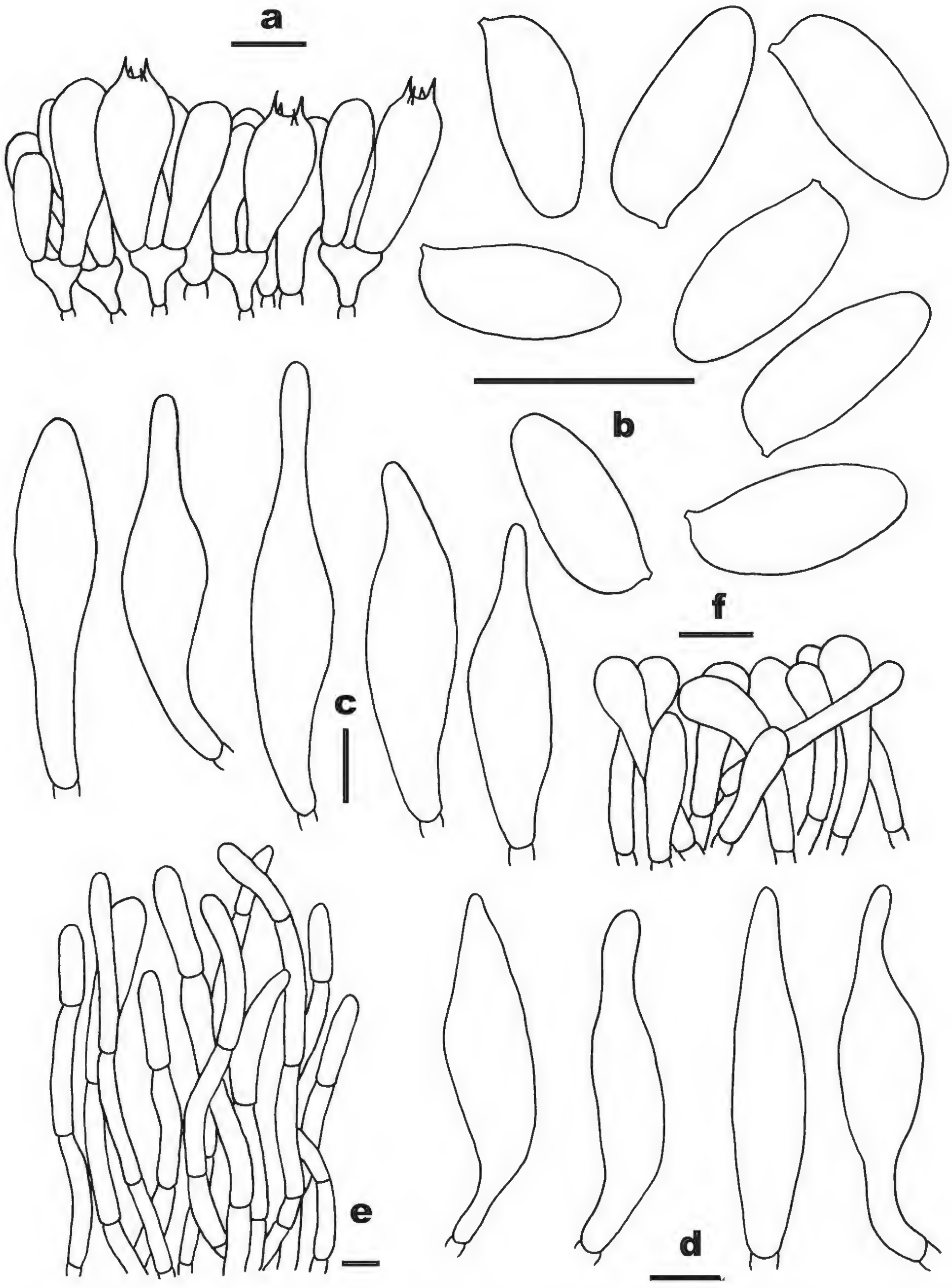


**Figure 4.** Microscopic features of *Chalciporus aurantiolepidotus* (FHMU7049, holotype). **a.** Basidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Pileipellis; **f.** Stipitipellis. Scale bars: 10 μm. Drawings by X.N. Li.

sterigmata 2–5.5 µm in length. ***Cheilocystidia*** 38–63 × 8–12 µm, fusiform or subfusiform, slightly thick-walled (up to 1 µm), colorless to pale yellow in KOH. ***Pleurocystidia*** 41–61 × 9–13 µm, fusiform or subfusiform, slightly thick-walled (up to 1 µm), pale yellow in KOH. ***Hymenophoral trama*** boletoid, colorless to yellowish in KOH, thin- to slightly thick-walled (up to 0.5 µm), 5–10 µm wide. ***Pileipellis*** a trichoderm 250–300 µm in thickness, composed of pale yellow in KOH, slightly thick-walled (up to 1 µm) hyphae; terminal cells 20–61 × 5–9 µm, clavate to subcylindrical or cystidioid. ***Pileus trama*** made up of hyphae 5–19 µm in diameter, thick-walled (up to 1.5 µm), yellow in KOH. ***Stipitipellis*** a trichoderm-like structure 150–200 µm thick, composed of hyaline to pale yellow in KOH, thin-walled hyphae; terminal cells 15–30× 4–7 µm, clavate or subcylindrical, occasionally subfusiform. ***Stipe trama*** composed of parallel hyphae 3–7 µm in diameter, cylindrical, thin-walled, yellow in KOH. ***Clamp connections*** absent in all tissues.

**Habitat.** Solitary or scattered on the ground in forests dominated by fagaceous trees (*Lithocarpus* spp.).

**Known distribution.** Southern China (Hainan Province), probably Guangdong Province, and Thailand (Fig. 1).

**Additional materials examined.** China • Hainan Province: Changjiang County, Bawangling of Hainan Tropical Rainforest National Park, alt. 650 m, 19.1°N, 109.2°E, 18 May 2022, N.K. Zeng7076 (FHMU7056; ZJMR330727230331); • Baisha County, Yinggeling of Hainan Tropical Rainforest National Park, alt. 650 m, 19.2°N, 109.5°E, 20 July 2022, N.K. Zeng7352 (FHMU7472).

**Notes.** *Chalciporus aurantiolepidotus* is phylogenetically related and morphologically similar to *C. brunneus*, *C. hainanensis* Ming Zhang & T.H. Li, and *C. vulparius*. However, *C. brunneus* has a pale brown to brown pileus, a yellow hymenophore, a stipe usually reddish at the apex, and an intricate trichodermal pileipellis (see below); *C. hainanensis* has a light orange-brown pileus, a white context changing red when bruised, and a stipe usually reddish at the apex (see below); *C. vulparius* has a tomentose, reddish-brown to pale reddish-brown pileus, a reddish-pink hymenophore, a stipe covered with white to brown scales, and shorter basidiospores measuring 5.5–9 × 3–5 µm (Xu et al. 2021).

### *Chalciporus brunneus* N.K. Zeng & X. Zhang, sp. nov.

MycoBank No: 860040

Figs 2f–h, 5

**Etymology.** Latin "*brunneus*", referring to the pale brown to brown pileus.

**Holotype.** China • Hainan Province, Changjiang County, Bawangling of Hainan Tropical Rainforest National Park, alt. 650 m, 19.2°N, 109.1°E, 13 May 2025, N.K. Zeng8522 (FHMU8246).

**Diagnosis.** Differs from closest species of *Chalciporus* by a pale brown to brown pileus, a yellowish-white context unchanging when bruised, a yellow hymenophore, a stipe usually reddish at the apex, and an intricate trichodermal pileipellis.

**Description.** ***Basidiomata*** very small to small-sized. ***Pileus*** 1.2–3.6 cm in diameter, subhemispherical to convex or plano-convex, margin incurved; surface slightly viscid when wet, pale brown to brown (6C2–6C3); context 0.2–0.7 cm

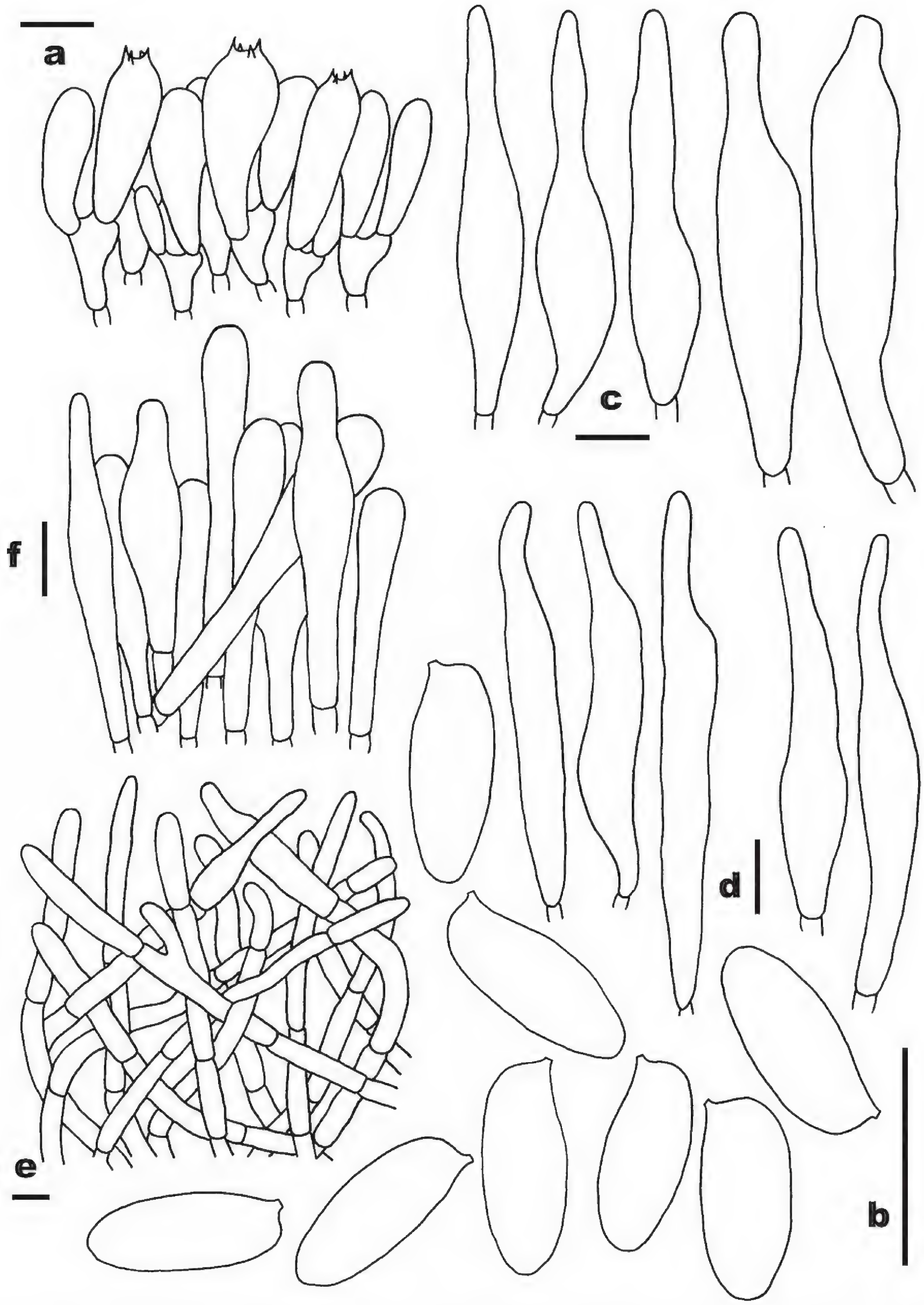


**Figure 5.** Microscopic features of *Chalciporus brunneus* (FHMU8246, holotype). **a.** Basidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Pileipellis; **f.** Stipitipellis. Scale bars: 10 μm. Drawings by X.N. Li.

in thickness in the center of the pileus, yellowish white (1A2), unchanging in color when bruised. ***Hymenophore*** poroid, slightly decurrent; pores roundish or angular, 0.15–0.25 cm wide, yellow (5A4), unchanging in color when bruised;

tubes approximately 0.3 cm long, yellowish orange (5A5), unchanging in color when bruised. ***Stipe*** 1.8–3.8 × 0.3–0.65 cm, central, solid, subcylindrical; surface smooth, usually reddish at the apex, yellowish white (1A2) in the upper part, gradually becoming brown (6B2) toward the base, with distinct reddish longitudinal striations; context yellowish white (1A2), unchanging in color when bruised; basal mycelium white. ***Odor*** indistinct. ***Taste*** mild.

***Basidiospores*** [160/8/4] (7)8–10.5(11) × 3–5 µm, Q= (1.70)1.90–3.00(3.33), $Q_m$ = 2.34 ± 0.31, yellowish brown in KOH, elongated to cylindrical, slightly thick-walled (0.8–1 µm), smooth under the light microscope. ***Basidia*** 19–30 × 6–9 µm, clavate, slightly thick-walled (up to 1 µm), 4-spored, colorless to pale yellow in KOH; sterigmata 2–4 µm in length. ***Cheilocystidia*** 33–65 × 5–11 µm, fusiform or subfusiform, slightly thick-walled (up to 1 µm), colorless in KOH. ***Pleurocystidia*** 33–71 × 6–9 µm, fusiform or subfusiform, slightly thick-walled (up to 1 µm), colorless in KOH. ***Hymenophoral trama*** boletoid, colorless to yellowish in KOH, thin- to slightly thick-walled (up to 0.5 µm), 4–10 µm wide. ***Pileipellis*** an intricate trichoderm 200–360 µm in thickness, composed of hyaline in KOH, slightly thick-walled (up to 1 µm) hyphae; terminal cells 8–69 × 4–8 µm, clavate to subcylindrical or cystidioid. ***Pileus trama*** made up of hyphae 4–20 µm in diameter, slightly thick-walled (up to 1 µm), colorless in KOH. ***Stipitipellis*** a trichoderm-like structure 150–300 µm thick, composed of hyaline to pale yellow in KOH, slightly thick-walled (up to 1 µm) hyphae; terminal cells 30–60× 5–6 µm, clavate or subcylindrical, occasionally subfusiform. ***Stipe trama*** composed of parallel hyphae 3–13 µm in diameter, cylindrical, thin- to slightly thick-walled (up to 1 µm), hyaline to pale yellow in KOH. ***Clamp connections*** absent in all tissues.

**Habitat.** Gregarious on the ground in forests dominated by fagaceous trees (*Lithocarpus* spp.).

**Known distribution.** Southern China (Hainan Province).

**Additional materials examined.** China • Hainan Province, Changjiang County, Bawangling of Hainan Tropical Rainforest National Park, alt. 650 m, 19.2°N, 109.1°E, 12 May 2025, N.K. Zeng8522-1 (FHMU11617); • same location and date, N.K. Zeng8522-2 (FHMU11547); • same location and date, N.K. Zeng8522-3 (FHMU11548).

**Notes.** *Chalciporus brunneus* is phylogenetically related to *C. aurantiolepidotus* and *C. hainanensis*. However, *C. hainanensis* has a light orange-brown pileus, a white context turning red when bruised, and a reddish-orange hymenophore (see below). The morphological differences between *C. brunneus* and *C. aurantiolepidotus* have been discussed above. Morphologically, *C. brunneus* is similar to *C. sinensis*. However, *C. sinensis* has a pileus covered with brown to grey-brown scales, shorter, subglobose to ellipsoid basidiospores measuring 4–7 × 3.5–5 µm, and a trichodermial pileipellis (Xu et al. 2021).

***Chalciporus citrinoaurantius*** **Ming Zhang & T.H. Li, Phytotaxa 327 (1): 49, 2017**
MycoBank No: 821522

**Known distribution.** Central (Hunan Province) and eastern China (Zhejiang Province) (Zhang et al. 2017).

**Holotype.** GDGM44776 (China, Hunan Province) (non vidi).

**Notes.** *Chalciporus citrinoaurantius* was originally described from Hunan Province of central China (Zhang et al. 2017); illustrations and a full description of the species have been provided by Zhang et al. (2017).

***Chalciporus hainanensis*** **Ming Zhang & T.H. Li, Phytotaxa 327 (1): 47–56, 2017**

MycoBank No: 821521

Figs 2i, 6

**Description.** ***Basidiomata*** very small-sized. ***Pileus*** 1–2 cm in diameter, sub-hemispherical to convex when young, plano-convex to applanate when mature; surface dry, tomentose, light orange-brown (5A3–5A4); context 0.2–0.5 cm in thickness in the center of the pileus, white (1A1), changing red when bruised. ***Hymenophore*** poroid, slightly decurrent; pores angular, about 0.1 cm wide, reddish orange (6A5–6A6); tubes about 0.2 cm long, reddish orange (6A5). ***Stipe*** 1.1–2.3 × 0.2 cm, central, solid, subcylindrical; surface orange-brown to brown (5B4–5B6), but reddish at the apex, with distinctly longitudinal striations; context white (1A1), changing red when bruised; basal mycelium white. ***Odor*** indistinct. ***Taste*** mild.

***Basidiospores*** [80/4/1] 7.5–10 × 3.5–5 µm, Q= (1.70)1.88–2.50(2.57), $Q_m$ = 2.16 ± 0.19, yellowish brown in KOH, elongated to cylindrical, thin-walled, smooth under the light microscope. ***Basidia*** 17–30 × 8–10.5 µm, clavate, thin-walled, 4-spored, colorless in KOH; sterigmata 3–5 µm in length. ***Cheilocystidia*** 17–31 × 6–12 µm, fusiform or subfusiform, slightly thick-walled (up to 1 µm), colorless in KOH. ***Pleurocystidia*** 22–35 × 7–10 µm, fusiform or subfusiform, slightly thick-walled (up to 1 µm), colorless in KOH. ***Hymenophoral trama*** boletoid, yellowish in KOH, thin- to slightly thick-walled (up to 0.5 µm), 3–11 µm wide. ***Pileipellis*** a trichoderm 200–350 µm in thickness, composed of pale yellow in KOH, slightly thick-walled (up to 1 µm) hyphae; terminal cells 20–65 × 7–9 µm, clavate to subcylindrical or cystidioid. ***Pileus trama*** made up of hyphae 1–9 µm in diameter, thin-walled, colorless to pale yellow in KOH. ***Stipitipellis*** a trichoderm-like structure 150–250 µm thick, composed of hyaline to pale yellow in KOH, slightly thin-walled (up to 1 µm) hyphae; terminal cells 10–30× 5–8 µm, clavate or subcylindrical, occasionally fusiform. ***Stipe trama*** composed of parallel hyphae 4–15 µm in diameter, cylindrical, thin-walled, yellow in KOH. ***Clamp connections*** absent in all tissues.

**Habitat.** Solitary or gregarious on the ground in forests dominated by fagaceous trees(*Castanopsis* spp., *Cyclobalanopsis* spp., *Lithocarpus* spp.).

**Known distribution.** Southern (Hainan Province) and southeastern China (Fujian Province).

**Holotype.** GDGM44464 (China, Hainan Province) (non vidi).

**Materials examined.** China • Fujian Province, Jiangle County, Longqishan National Nature Reserve, elev. 750 m alt. 650 m, 26.4°N, 117.2°E, 21 August 2023, N.K. Zeng8211 (FHMU9951); • Hainan Province, Baisha County, Yinggeling of Hainan Tropical Rainforest National Park, elev. 550 m, 26 June 2015, S. Jiang81 (FHMU4573).

**Notes.** *Chalciporus hainanensis* was originally described from Hainan Province of southern China (Zhang et al. 2017). In the present study, it was

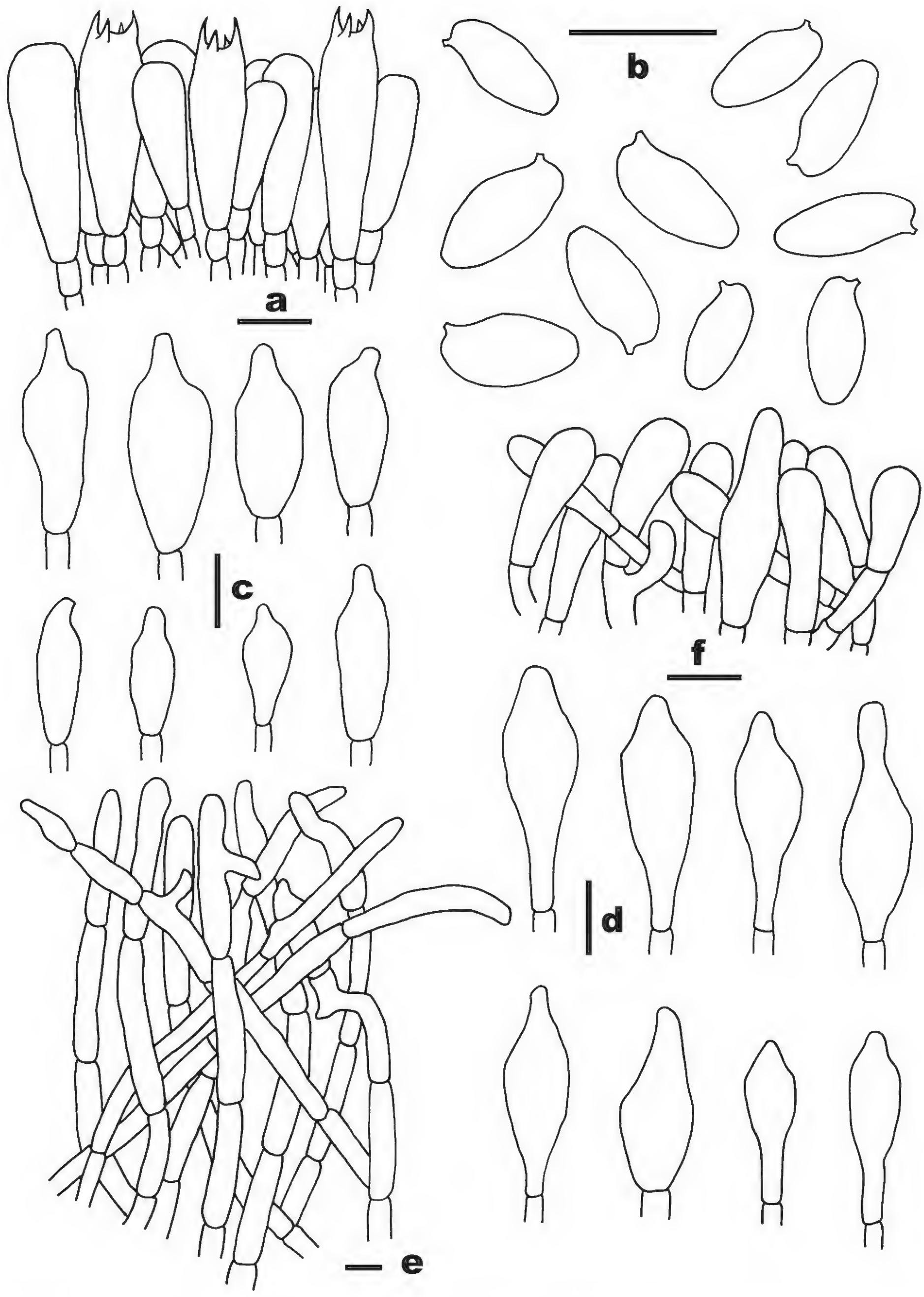


**Figure 6.** Microscopic features of *Chalciporus hainanensis* (FHMU9951). **a.** Basidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Pileipellis; **f.** Stipitipellis. Scale bars: 10 μm. Drawings by X.N. Li.

also found to be distributed in Fujian Province of southeastern China. The species is characterized by a very small basidioma, a tomentose, light orange-brown pileus, a reddish-orange hymenophore surface, and a trichodermal pileipellis.

***Chalciporus piperatus* (Bull.) Bataille, Bull. Soc. Hist. Nat. Doubs 15: 39, 1908**
MycoBank No: 311021

*Boletus piperatus* Bull., Herb. Fr. 10 (109–120): t. 451:2, 1790.
*Suillus piperatus* (Bull.) Poir., Rev. gén. pl.: 498, 1806.
*Leccinum piperatum* (Bull.) Gray, ANat. Arr. Brit. Pl. 1: 647, 1821.
*Viscipellis piperata* (Bull.) Quél., Enchir. Fung. Eur. Media Gallia Vig.: 157, 1886.
*Ixocomus piperatus* (Bull.) Quél., Fl. mycol. Fr.: 414, 1888.
*Ceriomyces piperatus* (Bull.) Murrill, Mycologia 1 (4): 150, 1909.

**Known distribution.** Northern China (Shanxi Province), Europe, and North America (Halling et al. 2004; Wu et al. 2014; Xu et al. 2021; Mao et al. 2023); probably southwestern China (Yunnan Province) (Fig. 1).

**Notes.** *Chalciporus piperatus* was originally described from Europe (Bataille 1908). It was also reported from Shanxi Province, northern China (Mao et al. 2023). Illustrations and a full description of the species have been provided by Moser (1983), Alessio (1985), Muñoz (2005), Šutara et al. (2009), and Mao et al. (2023). It should be noted that *C. pseudopiperatus*, described from Europe, has been considered morphologically close to *C. piperatus* and remains poorly separated based on macroscopic features (Klofac and Krisai-Greilhuber 2020). Although molecular data for *C. pseudopiperatus* exist, its phylogenetic position and taxonomic status have not been fully resolved, and it has been suggested that the species may be more widespread in Europe. Future studies including type and additional European materials will be essential to clarify the relationship between *C. piperatus* and *C. pseudopiperatus*.

***Chalciporus radiatus* Ming Zhang & T.H. Li, Mycoscience 57 (1): 21, 2015**
MycoBank No: 811750

**Known distribution.** Central (Hunan Province), eastern (Zhejiang Province), southeastern (Fujian Province), and southern China (Guangdong and Hainan Provinces) (Zhang et al. 2016; Chai et al. 2019).

**Holotype.** GDGM 43285 (China, Hunan Province) (non vidi).

**Materials examined.** China • Zhejiang Province, Qingyuan County, Zuoxi Town, elev. 600 m, 21 August 2024, N.K. Zeng10292 (FHMU8509); • same location and date, N.K. Zeng10296 (FHMU8989).

**Notes.** *Chalciporus radiatus* was originally described from Hunan Province of central China (Zhang et al. 2016), the Zhejiang specimens cited above extend the range of distribution. Illustrations and a full description of the species have been provided by Zhang et al. (2016) and Chai et al. (2019).

***Chalciporus roseus*** **N.K. Zeng & X. Zhang, sp. nov.**
MycoBank No: 860041
Figs 2j–l, 7

**Etymology.** Latin "*roseus*", referring to pinkinsh to dark reddish pileus.

**Holotype.** China • Hainan Province, Wuzhishan County, Wuzhishan of Hainan Tropical Rainforest National Park, alt. 600 m, 18.9°N, 109.5°E, 8 May 2024, N.K. Zeng8516 (FHMU7888).

**Diagnosis.** Differs from closest species of *Chalciporus* by a pinkish to dark reddish pileus with squamules, a yellow hymenophore bruising blue, a pale yellow context changing blue when bruised, broadly ellipsoid to elongate basidiospores measuring 4–5.5 × 3–3.5 µm, and a trichodermal pileipellis.

**Description.** ***Basidiomata*** small-sized. ***Pileus*** 2.8–4.1 cm in diameter, hemispherical to applanate; surface dry, pinkish to dark reddish (11A4–11B5), covered with squamules; context 0.3–0.7 cm in thickness in the center of the pileus, pale yellow (1A2), changing blue when bruised. ***Hymenophore*** poroid, slightly decurrent; pores subangular to roundish, 0.1–0.25 cm wide, yellow (1A4), changing blue in color when bruised; tubes yellowish, changing blue when bruised. ***Stipe*** 4.7–6.2 × 0.4–0.8 cm, central, solid, subcylindrical; surface pinkish to dark reddish (11A4–11B5), with distinctly longitudinal striations; context pale yellow (1A2), changing red when bruised; basal mycelium white. ***Odor*** indistinct. ***Taste*** mild.

***Basidiospores*** [60/3/3] (3.5)4–5.5(6) × (2.5)3–3.5(4) µm, Q= (1.14)1.17–1.83(2.0), $Q_m$ = 1.54 ± 0.18, yellowish brown in KOH, broadly ellipsoid, ellipsoid to elongate, slightly thick-walled (0.8–1 µm), smooth under the light microscope. ***Basidia*** 7–22 × 4–8 µm, clavate, thin-walled, 4-spored, colorless to pale yellow in KOH; sterigmata 2–6 µm in length. ***Cheilocystidia*** 26–44 × 5–9 µm, fusiform or subfusiform, slightly thick-walled (up to 1 µm), colorless to pale yellow in KOH. ***Pleurocystidia*** 19–43 × 5–8 µm, fusiform or subfusiform, thin-walled, colorless to pale yellow in KOH. ***Hymenophoral trama*** boletoid, colorless to yellowish in KOH, thin- to slightly thick-walled (up to 0.5 µm), 9–15 µm wide. ***Pileipellis*** a trichoderm 150–250 µm in thickness, composed of colorless to pale yellow in KOH, slightly thick-walled (up to 1 µm) hyphae; terminal cells 14–40 × 6–10 µm, clavate to subcylindrical or cystidioid. ***Pileus trama*** made up of hyphae 5–19 µm in diameter, slightly thick-walled (up to 1 µm), colorless in KOH. ***Stipitipellis*** a trichoderm-like structure 700–800 µm thick, composed of hyaline to pale yellow in KOH, thin-walled hyphae; terminal cells 10–29× 4.5–9 µm, clavate or subcylindrical. ***Stipe trama*** composed of parallel hyphae 3–7 µm diameter, cylindrical, thin-walled, yellow in KOH. ***Clamp connections*** absent in all tissues.

**Habitat.** Solitary or scattered on the ground in forests dominated by fagaceous trees (*Lithocarpus* spp.).

**Known distribution.** Southern China (Hainan Province).

**Additional materials examined.** China • Hainan Province: Wuzhishan County, Wuzhishan of Hainan Tropical Rainforest National Park, alt. 600 m, 18.9°N, 109.5°E, 8 May 2024, N.K. Zeng8516-1 (FHMU11614); • same location and date, N.K. Zeng8516-2 (FHMU11615).

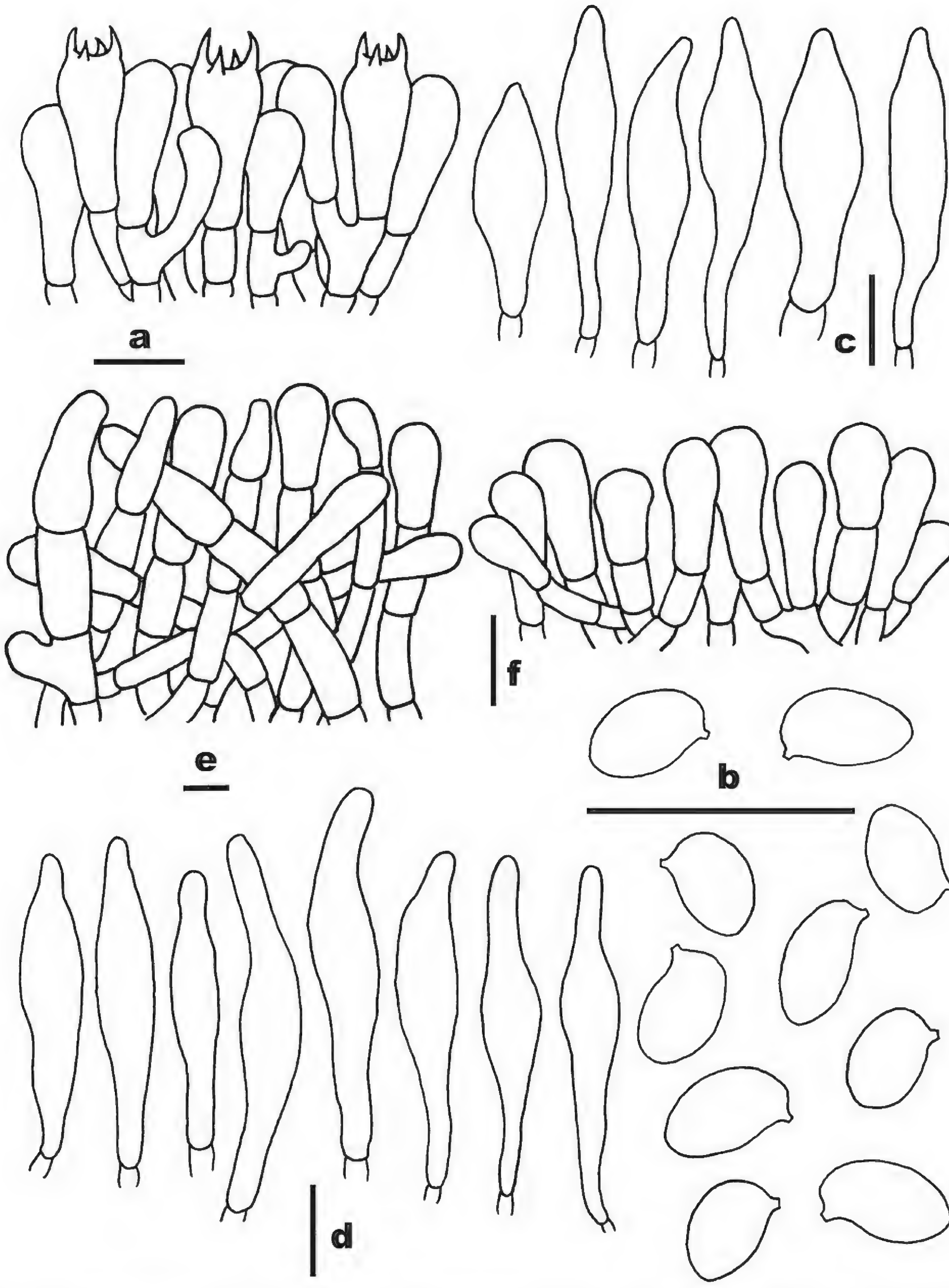


**Figure 7.** Microscopic features of *Chalciporus roseus* (FHMU7888, holotype). **a.** Basidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Pileipellis; **f** Stipitipellis. Scale bars: 10 μm. Drawings by X.N. Li.

**Notes.** Phylogenetically, *C. roseus* is closely related to lineage 5, which includes two collections from southwestern China (Fig. 1). However, since both specimens representing this lineage are immature, detailed morphological comparisons will

be performed in future studies when mature specimens become available. Morphologically, the feature of the dark reddish pileus and yellow hymenophoral surface of *C. roseus* distinguishes it from other species in the genus *Chalciporus*.

***Chalciporus rubinelloides*** **G.Wu & Zhu L. Yang, Fungal Diversity 81: 74, 2016**
MycoBank No: 818400

**Known distribution.** Southwestern China (Yunnan Province) (Wu et al. 2016).

**Holotype.** HKAS74952 (China, Yunnan Province) (non vidi).

**Notes.** *Chalciporus rubinelloides* was originally described from Yunnan Province of southwestern China (Wu et al. 2016); illustrations and a full description of the species have been provided by Wu et al. (2016).

***Chalciporus sinensis*** **N.K. Zeng, Chang Xu, S. Jiang & Zhi Q. Liang, Mycol. Progr. 20 (12): 1576, 2021**
MycoBank No: 839317

**Known distribution.** Southern China (Hainan Province) (Xu et al. 2021).

**Holotype.** N.K. Zeng4478 (FHMU4701) (China, Hainan Province) (vidi).

**Notes.** *Chalciporus sinensis* was originally described from Hainan Province of southern China (Xu et al. 2021); illustrations and a full description of the species have been provided by Xu et al. (Xu et al. 2021).

***Chalciporus vulparius*** **N.K. Zeng, Chang Xu & Zhi Q. Liang, Mycol. Progr. 20 (12): 1578, 2021**
MycoBank No: 839318

**Known distribution.** Southern China (Hainan Province) (Xu et al. 2021).

**Holotype.** N.K. Zeng4979 (FHMU5560) (China, Hainan Province) (vidi).

**Notes.** *Chalciporus vulparius* was originally described from Hainan Province of southern China (Xu et al. 2021); illustrations and a full description of the species have been provided by Xu et al. (Xu et al. 2021).

## Key to accepted *Chalciporus* species in China

1 Hymenophoral surface yellow ..... **2**
– Hymenophoral surface reddish-orange to reddish ..... **3**
2 Pileal surface pale brown to brown, tomentose, context unchanging in color when bruised ..... ***C. brunneus***
– Pileal surface pinkish to dark reddish, covered with squamules, context changing blue when bruised ..... ***C. roseus***
3 Pores arranged radially when young (appearing sublamellate at maturity) .... ..... ***C. radiatus***
– Pores not arranged radially ..... **4**
4 Pileal context changing pink or red when bruised ..... **5**
– Pileal context unchanging in color when bruised ..... **6**

5 Basidiospores 9–11 × 3–3.5 μm ..... ***C. piperatus***
– Basidiospores 7.5–10 × 3.5–5 μm ..... ***C. hainanensis***
6 Pileal surface distinctly squamulose (with scales or squamules) ..... **7**
– Pileal surface nearly glabrous, velvety-tomentose, or tomentose, without distinct scales or squamules ..... **8**
7 Pileal surface covered with brown to grey-brown scales ..... ***C. sinensis***
– Pileal surface covered with orange to reddish squamules ..... ***C. aurantiolepidotus***
8 Basidiomata small to medium (pileus up to 7 cm in diameter), basidiospores longer (up to16 μm long) ..... ***C. rubinelloides***
– Basidiomata very small to small (pileus up to 5 cm in diameter), basidiospores shorter (up to 13 μm long) ..... **9**
9 Pileal surface reddish brown to pale reddish brown, basidiospores shorter measuring 5.5–9 × 3–5 μm ..... ***C. vulparius***
– Pileal surface light yellow to greyish orange, basidiospores longer measuring 9.5–12.5 × 3.5–4 μm ..... ***C. citrinoaurantius***

***Pseudophylloporus*** **N.K. Zeng, H.Z. Qin, W.F. Lin & L.G. Hu, J. Fungi 10: 7. 2024**

*Pseudophylloporus*, typified by *P. baishanzuensis*, was initially established to accommodate species characterized by a lamellate hymenophore usually with forked lamellae (Qin et al. 2024). Until recently, the genus contained only a single known species, viz. *P. baishanzuensis*, which was uncovered in subtropical evergreen broad-leaved forests in eastern China. In the present study, a second species of *Pseudophylloporus* is described based on morphological features and phylogenetic evidence.

***Pseudophylloporus baishanzuensis*** **N.K. Zeng, H.Z. Qin, W.F. Lin & L.G. Hu, J. Fungi 10: 8, 2024**
MycoBank No: 855764

**Known distribution.** Eastern China (Zhejiang Province) (Qin et al. 2024).

**Holotype.** N.K. Zeng7702 (FHMU7694) (China, Zhejiang Province) (vidi).

**Notes.** *Pseudophylloporus baishanzuensis* was originally described from Zhejiang Province of eastern China (Qin et al. 2024); illustrations and a full description of the species have been provided by Qin et al. (2024).

***Pseudophylloporus castaneus*** **N.K. Zeng, X. Zhang & J.B. Pu, sp. nov.**
MycoBank No: 860042
Figs 2m–o, 8

**Etymology.** Latin "*castaneus*", referring to the chestnut-brown pileus.

**Holotype.** China • Zhejiang Province, Pan'an County, Dapanshan National Nature Reserve, alt. 1003 m, 29.0°N, 120.5°E, 7 July 2023, FC330727230331 (ZJMR330727230331).

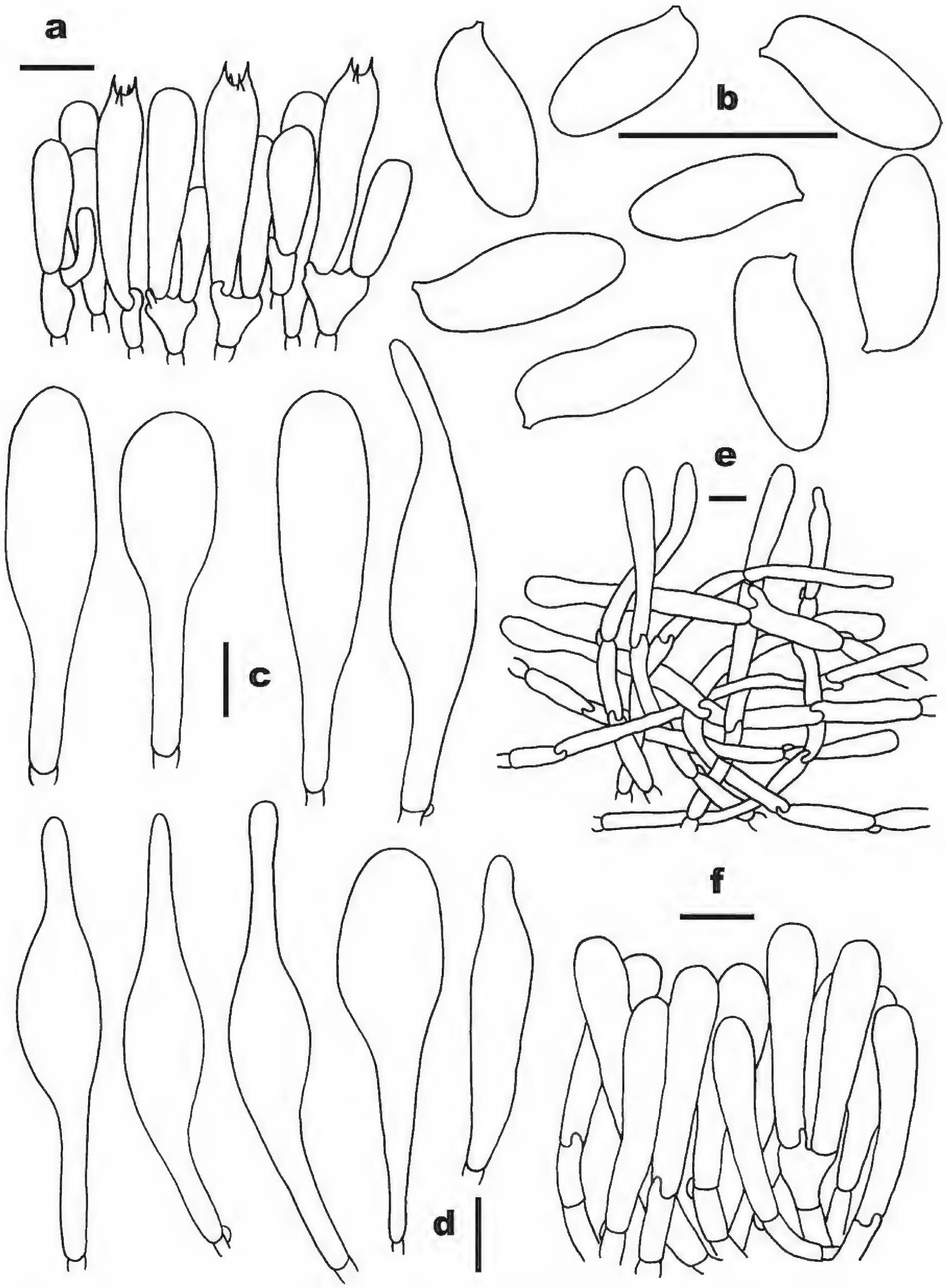


**Figure 8.** Microscopic features of *Pseudophylloporus castaneus* (ZJMR330727230331, holotype). **a.** Basidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Pileipellis; **f.** Stipitipellis. Scale bars: 10 μm. Drawings by X.N. Li.

**Diagnosis.** Differs from closest species of *Pseudophylloporus* by a chestnut-brown pileus, cystidia with golden or yellowish-brown plasmatic pigments, and an intricate trichodermal pileipellis.

**Description.** ***Basidiomata*** very small-sized. ***Pileus*** 2.5–3 cm in diameter, subhemispherical when young, then subhemispherical to plano-convex; surface dry, tomentose, chestnut-brown (5E7–5E8); context 0.3–0.6 cm in thickness in the center of the pileus, white (1A1), changing bluish when injured. ***Hymenophore*** lamellate, free; lamellae 0.1–0.3 cm in height, subdistant, usually forked, brown (5D4), turning blue quickly. ***Stipe*** 1.7–2.6 × 0.3–0.5 cm, clavate or tapering upwards, solid; surface yellow (4A3) to yellowish-brown (4C5), with purple-reddish (10E3) longitudinal striations; context pale yellow (2A2), changing blue slightly when injured; basal mycelium yellowish (2A4). ***Odor*** indistinct. ***Taste*** mild.

***Basidiospores*** [60/3/3] 8–9.5(10) × 3–4(4.5) µm, Q = 2.0–3.0, $Q_m$ = 2.44 ± 0.29, yellowish brown in KOH, fusoid to cylindrical, slightly thick-walled (0.8–1 µm), smooth under the light microscope. ***Basidia*** 24–34 × 5–8 µm, clavate, slightly thick-walled (0.8–1 µm), 4-spored, colorless to pale yellow in KOH; sterigmata 2–5 µm in length. ***Cheilocystidia*** 43–65 × 10–15 µm, abundant, ventricose, subclavate or subfusiform, slightly thick-walled (up to 1 µm), with golden or yellowish brown plasmatic pigment in KOH. ***Pleurocystidia*** 41–65 × 8–15 µm, subclavate or subfusiform, thin- to slightly thick-walled (up to 1 µm), with golden or yellowish brown plasmatic pigment in KOH. ***Hymenophoral trama*** boletoid, colorless to yellowish in KOH, thin- to slightly thick-walled (up to 0.5 µm), 4–17 µm wide. ***Pileipellis*** an intricate trichoderm 150–350 µm in thickness, composed of light yellow in KOH, slightly thick-walled (up to 1 µm) hyphae; terminal cells 25–95 × 4–9 µm, clavate to subcylindrical or cystidioid. ***Pileus trama*** made up of hyphae 4–10 µm in diameter, slightly thick-walled (up to 1 µm), yellow in KOH. ***Stipitipellis*** a trichoderm-like structure 30–100 µm thick, composed of pale yellow in KOH, slightly thick-walled (up to 1 µm) hyphae, terminal cells 30–60 × 5–6 µm, subclavate or clavate. ***Stipe trama*** composed of parallel hyphae 5–30 µm in diameter, cylindrical, thin- to slightly thick-walled (up to 0.5 µm), pale yellow in KOH. ***Clamp connections*** present in all tissues.

**Habitat.** Solitary or scattered on the ground in forests dominated by fagaceous trees (*Quercus* spp.)

**Known distribution.** Eastern China (Zhejiang Province).

**Additional materials examined.** China • Zhejiang Province, Pan'an County, Dapanshan National Nature Reserve, alt. 1003 m, 28.9°N, 120.5°E, 28 June 2023, FC330727230331-1 (FHMU11549); • same location and date, FC330727230331-2 (FHMU11550).

**Notes.** *Pseudophylloporus castaneus* is phylogenetically related and morphologically similar to *P. baishanzuensis*. However, *P. baishanzuensis* has a yellowish-brown to pale brown pileus, a stipe densely covered with pale brown scales, cystidia without golden or yellowish brown plasmatic pigments, and a cutis-type pileipellis (Qin et al. 2024).

## Key to accepted *Pseudophylloporus* species in China

1 Pileal suface chestnut-brown, stipe without pale brown scales, cystidia with golden or yellowish-brown plasmatic pigment, pileipellis trichodermal ..... ***P. castaneus***

– Pileal suface yellowish-brown to pale brown, stipe densely covered with pale brown scales, cystidia without golden or yellowish brown plasmatic pigment, pileipellis a cutis ..... ***P. baishanzuensis***

## Discussion

This study clearly reveals the species diversity and taxonomic composition of the subfamily Chalciporoideae in China. A total of 16 phylogenetic species-level lineages were identified, including 2 in *Buchwaldoboletus*, 12 in *Chalciporus*, and 2 in *Pseudophylloporus*. Further detailed morphological observations show four new species are described herein (3 in *Chalciporus* and 1 in *Pseudophylloporus*), and 10 known species are confirmed to occur in China (2 in *Buchwaldoboletus*, 7 in *Chalciporus*, and 1 in *Pseudophylloporus*) (Table 2). These results not only contribute to our pertinent knowledge of the Chalciporoideae subfamily but also provide a foundation for further studies on the subfamily's biogeography and ecological adaptation.

Chalciporoideae represents one of the earliest diverging lineages within Boletaceae, yet its classification has long been controversial. Recent phylogenetic studies have confirmed that *Chalciporus*, *Buchwaldoboletus*, and the newly defined genus *Pseudophylloporus* constitute a well-supported monophyletic group (Qin et al. 2024; Tremble et al. 2024). However, *Rubinoboletus* Pilát & Dermek was originally described as a monotypic genus, and its type species, *R. rubinus* (W.G. Sm.) Pilát & Dermek, has been conclusively shown to nest within *Chalciporus*, making *Rubinoboletus* a synonym of the latter. Nevertheless, the placement of other species that were subsequently assigned to *Rubinoboletus* remains unresolved. Based on early morphological studies, *Rubinoboletus* was considered synonymous with *Chalciporus* (Singer 1973; Pegler and Young 1981; Klofac 2006), with Klofac (2006) further proposing its treatment as a subgenus. Recent genome-scale analyses also confirmed that the type species of *Rubinoboletus*, *R. rubinus* (W.G. Sm.) Pilát & Dermek, belongs firmly within the *Chalciporus* clade, thus validating the synonymy of the two genera (Tremble et al. 2024). However, this taxonomic resolution does not extend to all species classified in *Rubinoboletus*. For instance, *R. phaseolisporus* T.H. Li, R.N. Hilton & Watling was reclassified into the genus *Tylopilus* P. Karst. based on a combi-

**Table 2.** List of described, reported or controversial Chalciporoideae species in China.

| Species | Type locality | Treatment | References |
|---|---|---|---|
| *Buchwaldoboletus lignicola* | Germany | Accepted | Pilát (1969); Wu et al. (2016) |
| *Buchwaldoboletus xylophilus* | Sri Lanka | Accepted | Ortiz-Santana and Both (2011); Xie et al. (2021) |
| *Chalciporus aurantiolepidotus* | Hainan, southern China | Accepted | This study |
| *Chalciporus brunneus* | Hainan, southern China | Accepted | This study |
| *Chalciporus citrinoaurantius* | Hunan, central China | Accepted | Zhang et al. (2017) |
| *Chalciporus hainanensis* | Hainan, southern China | Accepted | Zhang et al. (2017) |
| *Chalciporus piperatus* | Europe | Accepted | Bataille (1908); Mao et al. (2023) |
| *Chalciporus radiatus* | Hunan, central Chin | Accepted | Zhang et al. (2016); Zhang et al. (2017) |
| *Chalciporus roseus* | Hainan, southern China | Accepted | This study |
| *Chalciporus rubinelloides* | Yunnan, SW China | Accepted | Wu et al. (2016) |
| *Chalciporus sinensis* | Hainan, southern China | Accepted | Xu et al. (2021) |
| *Chalciporus vulparius* | Hainan, southern China | Accepted | Xu et al. (2021) |
| *Rubinoboletus ballouii* | Singapore | Transferred to *Tylopilus* | Singer (1947) |
| *Rubinoboletus ballouii* var. *fuscatus* | Singapore | Transferred to *Tylopilus* | Heinemann and Rammeloo (1983); Li and Yang (2021) |
| *Pseudophylloporus baishanzuensis* | Zhejiang, eastern China | Accepted | Qin et al. (2024) |
| *Pseudophylloporus castaneus* | Zhejiang, eastern China | Accepted | This study |

nation of morphological characteristics and multilocus phylogenetic analyses (Osmundson et al. 2021). The reclassification of *Rubinoboletus* highlights its polyphyletic nature and emphasizes the necessity of conducting species-level systematic analyses across the genus. Additionally, the genus *Nevesoporus* A.C. Magnago & T.W. Henkel was originally placed within the subfamily Chalciporoideae at the time of its establishment (Magnago et al. 2022). However, subsequent genome-scale analyses and multilocus phylogenetic studies have confirmed that this genus should be assigned to Boletoideae rather than Chalciporoideae (Osmundson et al. 2021; Qin et al. 2024). These findings underscore the necessity of establishing a comprehensive taxonomic framework that integrates morphological, molecular, and ecological evidence to achieve more accurate phylogenetic placement and taxonomic refinement.

Our study also highlights unexpected morphological diversity within the genus *Chalciporus*. Traditionally, the presence of a distinctly reddish hymenophore has been regarded as one of the key diagnostic features of the genus. However, exceptions are known, such as *C. hypochryseus* described by Šutara (1993), which is characterized by yellow pores, a feature also documented by subsequent authors (Galli 1998; Simonini 1998; Muñoz 2005; Šutara et al. 2009). Consistent with this, our newly described species, *C. brunneus* and *C. roseus*, also exhibit a pale-yellow to yellow hymenophore, differing significantly from the conventional reddish pigmentation. The discovery of these taxa further suggests that the current generic concept of *Chalciporus* may need to be revised or expanded to accommodate a wider spectrum of hymenophore coloration.

Notably, many species in the Boletaceae exhibit pronounced geographic restriction, with truly widespread taxa being relatively rare (Chai et al. 2019; Xie et al. 2021; Xue et al. 2023; Qin et al. 2024). *Chalciporus piperatus*, originally described from Europe, has been widely reported in China based solely on morphological characters (Bi et al. 1993; Li and Song 2002), which has long raised doubts about its actual presence in the region (Xu et al. 2021). Recently, Mao et al. (2023) confirmed its occurrence in northern China (Shanxi Province) using both morphological and molecular phylogenetic evidence. Interestingly, in our phylogenetic analyses, sequences from Chinese specimens clustered with those from Germany, albeit with relatively low statistical support (Fig. 1). Given the geographic distribution pattern of *C. piperatus*, it is plausible that the European species *C. pseudopiperatus*, closely related to *C. piperatus* (Klofac and Krisai-Greilhuber 2020), may also occur in China. Therefore, further sampling and reassessment of specimens currently labelled as "*C. piperatus*" from China are strongly recommended.

Our study further highlights the remarkable diversity of Chalciporoideae in southern China, particularly in subtropical and tropical regions. The majority of species in this subfamily exhibit narrow geographic distributions, and the newly identified taxa are predominantly located in the same climatic zones. This distribution pattern suggests that the subtropical-tropical region of China represents a primary center of species diversity for Chalciporoideae. An exceptional case within our study is *B. lignicola*, the only species found to occur widely across both temperate and tropical regions of China. Its broad ecological amplitude and saprophytic or possibly mycoparasitic lifestyle suggest that it may hold potential for artificial cultivation.

Despite significant advances in recent years, the trophic modes of Chalciporoideae remain poorly understood. Members of this subfamily may adopt a range of nutritional strategies, including ectomycorrhizal, saprotrophic, and mycoparasitic lifestyles. Although some studies have suggested that species such as *C. piperatus* and *B. lignicola* may not be ectomycorrhizal (Dickie and Johnston 2008; Dickie et al. 2010; Robinson 2010), there is still a lack of systematic understanding of the subfamily's overall ecological traits. To elucidate its trophic spectrum, further integrative ecological studies will be necessary. Such investigations are not only essential for revealing the ecological plasticity within Chalciporoideae but also for enhancing our understanding of the evolutionary dynamics of nutritional modes in early-diverging bolete lineages.

In conclusion, this study provides new insights into the species diversity and phylogenetic relationships of Chalciporoideae in China. The discovery of novel taxa and the confirmation of known species distributions underscore the importance of subtropical and tropical China as a biodiversity hotspot for the subfamily. Continued extensive field surveys, coupled with integrative taxonomic and multidisciplinary approaches, will be vital for fully uncovering the ecological and evolutionary complexity of this important fungal group.

## Conclusion

Although a number of species within Chalciporoideae have been reported worldwide, the diversity and phylogenetic relationships of this subfamily remain insufficiently understood, especially in China. In the present study, four new species of Chalciporoideae were described, two previously known species were redescribed, and an additional eight known species were reviewed based on morphological characteristics and molecular phylogenetic analyses. Our findings provide new insights into the species composition within Chalciporoideae, significantly enhancing our understanding of the Boletaceae family in China.

## Acknowledgments

The first author is very grateful to Chun-Xia Zhang, Yunnan Institute of Tropical Crops, for providing the specimens. Thanks are due to Dapanshan National Park, Yinggeling Branch of Hainan Tropical Rainforest National Park Administration, Wuzhishan Branch of Hainan Tropical Rainforest National Park Administration and Bawangling Branch of Hainan Tropical Rainforest National Park Administration for their kind help during the field investigations.

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Use of AI

No use of AI was reported.

## Funding

This research was funded by the Special Fund Project for Environmental Protection of Hainan Province: Investigation and Assessment of Biodiversity in Wuzhishan City and Changjiang County, which was established by the Department of Ecology and Environment of Hainan Province; Central Grassland Ecological Protection and Restoration Funds–Comprehensive Resource Survey Project of Dapan Mountain Reserve (No. PACGZT2022-CS-005); Zhejiang Key Discipline in Traditional Chinese Medicine for Pharmaceutical Botany (No. 2024-XK-06); Zhejiang Provincial Department of Science and Technology Research Institute Support Program (No. KJTYSZX2025); and the Innovation and Entrepreneurship Training Program for College Students in Hainan Province, China (No. S202411658026).

## Author contributions

Conceptualization: Jin-Bao Pu and Nian-Kai Zeng; methodology, performing the experiment, and formal analysis: Xu Zhang, Xin-Ni Li, Xiao-Jun Wu, and Si-Yu Chen; resources: Nian-Kai Zeng, Jin-Bao Pu, Xiao-Dong Mu, Ye-Fei Yu, and Wei-Qing Liang; writing—original draft preparation: Xu Zhang; writing—review and editing: Jin-Bao Pu and Nian-Kai Zeng; supervision: Nian-Kai Zeng; project administration: Nian-Kai Zeng; funding acquisition: Jin-Bao Pu and Nian-Kai Zeng All authors have read and agreed to the published version of the manuscript.

## Author ORCIDs

Xu Zhang https://orcid.org/0000-0003-1283-0573
Xin-Ni Li https://orcid.org/0009-0000-8069-5241
Wei-Qing Liang https://orcid.org/0009-0003-2948-0845
Xiao-Dong Mu https://orcid.org/0009-0009-9375-0727
Ye-Fei Yu https://orcid.org/0009-0003-4890-5845
Xiao-Jun Wu https://orcid.org/0009-0001-4184-6331
Si-Yu Chen https://orcid.org/0009-0003-6597-3081
Jin-Bao Pu https://orcid.org/0000-0003-4911-1169
Nian-Kai Zeng https://orcid.org/0000-0001-7651-4524

## Data availability

All of the data that support the findings of this study are available in the main text.

## References

Alessio CL (1985) *Boletus* Dill. ex L. (*sensu lato*). Fungi Europaei (Vol. 2). Libreria editrice Biella Giovanna, Saronno, 705 pp.

An DY, Liang ZQ, Jiang S, Su MS, Zeng NK (2017) *Cantharellus hainanensis*, a new species with a smooth hymenophore from tropical China. Mycoscience 58(6): 438–444. https://doi.org/10.1016/j.myc.2017.06.004

Antonio C (2003) The complete mushroom book. Quadrille, London, 34 pp.

Aryal HP, Budathoki U (2013) *Buchwaldoboletus lignicola* (Basidiomycetes), an inedible wild mushroom new to Nepal. Our Nature 11(1): 31–35. https://doi.org/10.3126/on.v11i1.8241

Ayala-Vásquez O, Martínez-Reyes M, Pérez-Moreno J, Martínez-González CR, Pinzón JP, de la Fuente JI, Castro-Rivera R, García-Jiménez J, Balbuena-Carrasco S, Ramírez-Carbajal E, Yu F (2023) Five new species of *Aureoboletus* and *Chalciporus* (Boletace-

ae, Boletales) and their Ethnomycological aspects. Journal of Fungi 9(10): e1041. https://doi.org/10.3390/jof9101041

Baroni TJ, Both EE (1991) *Chalciporus piperatoides* in North America. Mycologia 83: 559–564. https://doi.org/10.1080/00275514.1991.12026055

Bas C (1969) Morphology and subdivision of *Amanita* and a monograph of its section Lepidella. Persoonia 5(4): 285–579.

Bataille F (1908) Quelques champignons intéressants des environs de Besançon. Bulletin de la Société d'Histoire Naturelle du Doubs 15: 23–61.

Bi ZS, Zheng GY, Li TH (1993) The Macrofungus Flora of China's Guangdong Province. Columbia University Press, New York, 756 pp.

Bidartondo MI, Ameri G, Döring H (2009) Closing the mycorrhizal DNA sequence gap. Mycological Research 113: 1025–1026. https://doi.org/10.1016/j.mycres.2009.09.009

Binder M, Hibbett DS (2006) Molecular systematics and biological diversification of Boletales. Mycologia 98(6): 971–981. https://doi.org/10.3852/mycologia.98.6.971

Caiafa MV, Smith ME (2022) Polyphyly, asexual reproduction and dual trophic mode in *Buchwaldoboletus*. Fungal Ecology 56: e101141. https://doi.org/10.1016/j.funeco.2022.101141

Chai H, Liang ZQ, Xue R, Jiang S, Luo SH, Wang Y, Wu LL, Tang LP, Chen Y, Hong D, Zeng NK (2019) New and noteworthy boletes from subtropical and tropical China. MycoKeys 46: 55–96. https://doi.org/10.3897/mycokeys.46.31470

Corner EJH (1972) *Boletus* in Malaysia. Government Printing Office, Singapore, 263 pp.

Degreef J, De Kesel AD (2008) *Chalciporus africanus*, a new bolete species from Africa. Mycotaxon 103: 329–335.

Deng CY, Kang C, Li Q, Xia YP (2018) Research on macrofungi in Caohai I: Species diversity. Guizhou Science 36(1): 5–15.

Desjardin DE, Binder M, Roekring S, Flegel T (2009) *Spongiforma*, a new genus of gasteroid boletes from Thailand. Fungal Diversity 37: 1–8.

Dickie IA, Johnston PR (2008) Invasive Fungi Research Priorities, with a Focus on *Amanita muscaria*. Landcare Research, Lincoln, New Zealand, 22 pp.

Dickie IA, Bolstridge N, Cooper JA, Peltzer DA (2010) Co-invasion by *Pinus* and its mycorrhizal fungi. The New Phytologist 187(2): 475–484. https://doi.org/10.1111/j.1469-8137.2010.03277.x

Dickie IA, Nuñez MA, Pringle A, Lebel T, Tourtellot SG, Johnston PR (2016) Towards management of invasive ectomycorrhizal fungi. Biological Invasions 18(12): 3383–3395. https://doi.org/10.1007/s10530-016-1243-x

Edgar RC (2004) MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Frank JL, Siegel N, Schwarz CF, Araki B, Vellinga EC (2020) *Xerocomellus* (Boletaceae) in western North America. Fungal Systematics and Evolution 6: 265–288. https://doi.org/10.3114/fuse.2020.06.13

Galli R (1998) I Boleti. Atlante pratico-monographico per la determinazione dei boleti. Edinatura, Milano.

Gómez LD (1996) Basidiomicetes de Costa Rica: *Xerocomus*, *Chalciporus*, *Pulveroboletus*, *Boletellus*, *Xanthoconium* (Agaricales: Boletaceae). Revista de Biología Tropical 44(Suppl 4): 59–89.

Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Halling RE, Mata M, Mueller GM (2004) Three new boletes for Costa Rica. Memoirs of the New York Botanical Garden 89: 141–147.

Halling RE, Nuhn M, Fechner NA, Osmundson TW, Soytong K, Arora D, Hibbett DS, Binder M (2012) *Sutorius*: A new genus for *Boletus eximius*. Mycologia 104(4): 951–961. https://doi.org/10.3852/11-376

Heinemann P, Rammeloo J (1983) Combinaisons et taxons nouveaux de Gyrodontaceae (Boletineae). Bulletin du Jardin Botanique National de Belgique 53: 294–297. https://doi.org/10.2307/3668043

Hosen MI, Feng B, Wu G, Zhu XT, Li YC, Yang ZL (2012) *Borofutus*, a new genus of Boletaceae from tropical Asia: Phylogeny, morphology and taxonomy. Fungal Diversity 58: 215–226. https://doi.org/10.1007/s13225-012-0211-8

Huelsenbeck JP, Ronquist F (2005) Bayesian analysis of molecular evolution using MrBayes. In: Nielsen R (Ed.) Statistical Methods in Molecular Evolution. Springer, New York, 183–226. https://doi.org/10.1007/0-387-27733-1_7

James TY, Kauff F, Schoch CL, Matheny PB, Hofstetter V, Cox CJ, Celio G, Gueidan C, Fraker E, Miadlikowska J, Lumbsch HT, Rauhut A, Reeb V, Arnold AE, Amtoft A, Stajich JE, Hosaka K, Sung GH, Johnson D, O'Rourke B, Crockett M, Binder M, Curtis JM, Slot JC, Wang Z, Wilson AW, Schüssler A, Longcore JE, O'Donnell K, Mozley-Standridge S, Porter D, Letcher PM, Powell MJ, Taylor JW, White MM, Griffith GW, Davies DR, Humber RA, Morton JB, Sugiyama J, Rossman AY, Rogers JD, Pfister DH, Hewitt D, Hansen K, Hambleton S, Shoemaker RA, Kohlmeyer J, Volkmann-Kohlmeyer B, Spotts RA, Serdani M, Crous PW, Hughes KW, Matsuura K, Langer E, Langer G, Untereiner WA, Lücking R, Büdel B, Geiser DM, Aptroot A, Diederich P, Schmitt I, Schultz M, Yahr R, Hibbett DS, Lutzoni F, McLaughlin DJ, Spatafora JW, Vilgalys R (2006) Reconstructing the early evolution of the fungi using a six-gene phylogeny. Nature 443(7113): 818–822. https://doi.org/10.1038/nature05110

Jo JW, Kwag YN, Cho SE, Han SK, Han JG, Lim YW, Sung GH, Oh SH, Kim CS (2019) First report of *Buchwaldoboletus lignicola* (Boletaceae), a potentially endangered basidiomycete species, in South Korea. Mycobiology 47(4): 521–526. https://doi.org/10.1080/12298093.2019.1682907

Kallenbach F (1929) *Boletus lignicola*. Die Pilze Mitteleuropas, Band 1, Die Röhrlinge (Boletaceae), 56–60.

Klofac W (2006) The genus *Chalciporus*, a world-wide survey. Österreichische Zeitschrift für Pilzkunde 15: 31–65.

Klofac W, Krisai-Greilhuber I (2020) *Chalciporus pseudopiperatus*, a new taxon in the *Chalciporus piperatus* species complex. Österreichische Zeitschrift für Pilzkunde 28: 75–78.

Kornerup A, Wanscher JH (1981) Taschenlexikon der Farben (3rd ed.). Muster-Schmidt Verlag, Zürich & Göttingen, 242 pp.

Li TH, Song B (2002) Species and distributions of Chinese edible boletes. Acta Edulis Fungi 9(2): 22–30. https://doi.org/10.16488/j.cnki.1005-9873.2002.02.006

Li YC, Yang ZL (2021) The Boletes of China: *Tylopilus* s.l. Science Press & Springer Nature Singapore, Beijing & Singapore, 418 pp. https://doi.org/10.1007/978-981-16-2986-0

Magnago AC, Alves-Silva G, Henkel TW, da Silveira RMB (2022) New genera, species, and combinations of Boletaceae from Brazil and Guyana. Mycologia 114(3): 607–625. https://doi.org/10.1080/00275514.2022.2037307

Mao N, Zhao TY, Zhang YX, Li T, Lv JC, Fan L (2023) Boletaceae from Shanxi Province of northern China with descriptions of ten new species. Mycosphere: Journal of Fungal Biology 14(1): 2013–2091. https://doi.org/10.5943/mycosphere/14/1/24

Matheny PB (2005) Improving phylogenetic inference of mushrooms with *RPB*1 and *RPB*2 nucleotide sequences (Inocybe; Agaricales). Molecular Phylogenetics and Evolution 35(1): 1–20. https://doi.org/10.1016/j.ympev.2004.11.014

Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo JM, Ge ZW, Yang ZL, Slot JC, Ammirati JF, Baroni TJ, Bougher NL, Hughes KW, Lodge DJ, Kerrigan RW, Seidl MT, Aanen DK, DeNitis M, Daniele GM, Desjardin DE, Kropp BR, Norvell LL, Parker A, Vellinga EC, Vilgalys R, Hibbett DS (2006) Major clades of Agaricales: A multilocus phylogenetic overview. Mycologia 98(6): 982–995. https://doi.org/10.3852/mycologia.98.6.982

Migliorini D, Capretti P, Santini A (2012) Caratterizzazione morfo-fisiologica ed analisi di alcuni aspetti ecologici di *Buchwaldoboletus lignicola*. Micologia Italiana 41: 45–52.

Miller MA, Pfeiffer W, Schwartz T (2011) The CIPRES Science Gateway: a community resource for phylogenetic analyses. In: Towns J, Brown S, Katz DS (Eds) Proceedings of the 2011 TeraGrid Conference: Extreme Digital Discovery. ACM, New York, NY, 41 pp. https://doi.org/10.1145/2016741.2016785

Morehouse EA, James TY, Ganley AR, Vilgalys R, Berger L, Murphy PJ, Longcore JE (2003) Multilocus sequence typing suggests the chytrid pathogen of amphibians is a recently emerged clone. Molecular Ecology 12(2): 395–403. https://doi.org/10.1046/j.1365-294X.2003.01732.x

Moreno G, García-Bona LM (1976) Macromycetos interesantes de Navarra. I. Anales del Instituto Botánico Cavanilles 33: 125–133.

Moser M (1983) Keys to Agarics and Boleti (Polyporales, Boletales, Agaricales, Russulales). Roger Phillips, London, 535 pp.

Muñoz JA (2005) *Boletus s. l.* Fungi Europaei (Vol. 1). Edizioni Candusso, Alassio, 951 pp.

Nanu S, Kumar TKA (2022) *Buchwaldoboletus xylophilus*, a boletoid fungus new to India. Studies in Fungi 7: 1–13. https://doi.org/10.48130/SIF-2022-0013

Nanu S, Kumar TKA (2024) New species of *Chalciporus* and *Tylopilus* from India, with keys to the known species. Mycologia 116(5): 729–743. https://doi.org/10.1080/00275514.2024.2358942

Nuhn ME, Binder M, Taylor AFS, Halling RE, Hibbett DS (2013) Phylogenetic overview of the Boletineae. Fungal Biology 117(7–8): 479–511. https://doi.org/10.1016/j.funbio.2013.04.008

Nylander JAA (2004) MrModeltest v2.3. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.

Ortiz-Santana B, Both EE (2011) A preliminary survey of the genus *Buchwaldoboletus* (Boletales: Boletaceae). Bulletin of the Buffalo Society of Natural Sciences 40: 1–14.

Osmundson TW, Bougher NL, Robinson RM, Halling RE (2021) *Rubinoboletus phaseolisporus* (Boletaceae) from Western Australia is a Tylopilus with bean-shaped spores. Nuytsia 32: 87–97. https://doi.org/10.58828/nuy01004

Pegler DN (1983) Agaric Flora of the Lesser Antilles; Additional Series IX; Kew Bulletin, London, UK, 668 pp.

Pegler DN (1986) Agaric flora of Sri Lanka. Kew Bulletin Additional Series 12: 1–519.

Pegler DN, Young TWK (1981) A natural arrangement of the Boletales, with reference to spore morphology. Transactions of the British Mycological Society 76(1): 103–146. https://doi.org/10.1016/S0007-1536(81)80013-7

Petch T (1922) Additions to Ceylon fungi II. Annals of the Royal Botanic Gardens, Peradeniya 7: 279–322.

Pilát A (1969) *Buchwaldoboletus*, genus novum Boletacearum. Friesia 9(1–2): 217–218.

Putra IP, Nurhayat OD, Sibero MT, Hermawan R (2025) Records on potentially endangered macrofungus (*Buchwaldoboletus lignicola*) in Indonesia. Comprehensive Plant Biology 49(1): 15–22. https://doi.org/10.2298/CPB2501015P

Qin HZ, Wang Y, Lin WF, Zeng H, Hu LG, Ke BR, Zeng ZH, Liang ZQ, Zeng NK (2024) *Pseudophylloporus* gen. nov. and *Rubroleccinum* gen. nov., two new genera revealed by morphological and phylogenetic evidences in the family Boletaceae from subtropical China. Journal of Fungi 10(12): e817. https://doi.org/10.3390/jof10120817

Raspé O, Vadthanarat S, De Kesel AD, Degreef J, Hyde KD, Lumyong S (2016) *Pulveroboletus fragrans*, a new Boletaceae species from Northern Thailand, with a remarkable aromatic odor. Mycological Progress 15: 1–8. https://doi.org/10.1007/s11557-016-1179-7

Roberts P, Evans S (2011) The Book of Fungi: A Life-Size Guide to Six Hundred Species from Around the World. University of Chicago Press, Chicago, IL, 656 pp. https://doi.org/10.7208/chicago/9780226177199.001.0001

Robinson R (2010) First record of *Amanita muscaria* in Western Australia. Australasian Mycologist 29: 4–6.

Simonini G (1998) Qualche specie rara o poco conosciuta della famiglia Boletaceae. Fungi non delineati (Vol. 6). Libreria Mykoflora, Alassio, 56 pp.

Singer R (1947) The Boletoideae of Florida: The Boletineae of Florida with notes on extralimital species III. American Midland Naturalist 37(1): 1–135. https://doi.org/10.2307/2421647

Singer R (1973) Notes on bolete taxonomy. Persoonia 7(2): 313–320.

Smith SA, Dunn CW (2008) Phyutility: A phyloinformatics tool for trees, alignments and molecular data. Bioinformatics 24(5): 715–716. https://doi.org/10.1093/bioinformatics/btm619

Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22(21): 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Šutara J (1993) *Boletus hypochryseus*, nový hrib ze skupiny druhu *Boletus piperatus*.–. Česká Mykologie 46: 203–208. https://doi.org/10.33585/cmy.46303

Šutara J, Mikšík M, Janda V (2009) Hřibovité houby. Čeled' Boletaceae a rody Gyrodon, Gyroporus, Boletinus a Suillus. Academia, Praha.

Tremble K, Henkel T, Bradshaw A, Domnauer C, Brown LM, Thám LX, Furci G, Aime MC, Moncalvo JM, Dentinger B (2024) A revised phylogeny of Boletaceae using whole genome sequences. Mycologia 116(3): 392–408. https://doi.org/10.1080/00275514.2024.2314963

Vadthanarat S, Amalfi M, Halling RE, Bandala V, Lumyong S, Raspé O (2019) Two new *Erythrophylloporus* species (Boletaceae) from Thailand, with two new combinations of American species. MycoKeys 55: 29–57. https://doi.org/10.3897/mycokeys.55.34570

Venturella G (2017) *Buchwaldoboletus lignicola* (Boletaceae), a rare basidiomycete from Europe. Plant Biosystems 151(4): 574–576. https://doi.org/10.1080/11263504.2017.1313791

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172(8): 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

White TJ, Bruns T, Lee SB, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR Protocols: A Guide to Methods and Applications. Academic Press, New York, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wu G, Feng B, Xu JP, Zhu XT, Li YC, Zeng NK, Hosen MI, Yang ZL (2014) Molecular phylogenetic analyses redefine seven major clades and reveal 22 new generic clades in the fungal family Boletaceae. Fungal Diversity 69(1): 93–115. https://doi.org/10.1007/s13225-014-0283-8

Wu G, Li YC, Zhu XT, Zhao K, Han LH, Cui YY, Li F, Xu JP, Yang ZL (2016) One hundred noteworthy boletes from China. Fungal Diversity 81(1): 25–188. https://doi.org/10.1007/s13225-016-0375-8

Wu G, Li HJ, Horak E, Wu K, Li GM, Yang ZL (2023) New taxa of Boletaceae from China. Mycosphere: Journal of Fungal Biology 14(1): 745–776. https://doi.org/10.5943/mycosphere/14/1/9

Xie HJ, Zhang CX, He MX, Liang ZQ, Deng XH, Zeng NK (2021) *Buchwaldoboletus xylophilus* and *Phlebopus portentosus*, two non-ectomycorrhizal boletes from tropical China. Phytotaxa 520(2): 137–154. https://doi.org/10.11646/phytotaxa.520.2.2

Xu C, Liang ZQ, Xie HJ, Jiang S, Fu XH, Zeng NK (2021) Two new species of *Chalciporus* (Boletaceae, Boletales) from tropical China. Mycological Progress 20(12): 1573–1582. https://doi.org/10.1007/s11557-021-01753-1

Xue R, Zhang X, Xu C, Xie HJ, Wu LL, Wang Y, Tang LP, Hao YJ, Zhao K, Jiang S, Li Y, Yang YY, Li Z, Liang ZQ, Zeng NK (2023) The subfamily Xerocomoideae (Boletaceae, Boletales) in China. Studies in Mycology 106: 95–197. https://doi.org/10.3114/sim.2022.106.03

Yang T, Mu H, Dai L, Liu J, Xu X, Gao F, Fang Y, Jian S, He M, Zhang C (2025) First report on the artificial cultivation techniques of *Buchwaldoboletus xylophilus* (Boletales, Boletaceae, *Buchwaldoboletus*) in Southwest China. Journal of Fungi 11(3): e172. https://doi.org/10.3390/jof11030172

Zhang M, Wang CQ, Li TH, Song B (2016) A new species of *Chalciporus* (Boletaceae, Boletales) with strongly radially arranged pores. Mycoscience 57(1): 20–25. https://doi.org/10.1016/j.myc.2015.07.004

Zhang M, Li TH, Song B (2017) Two new species of *Chalciporus* (Boletaceae) from southern China revealed by morphological characters and molecular data. Phytotaxa 327(1): 47–56. https://doi.org/10.11646/phytotaxa.327.1.2

Zhang Y, Mo MZ, Yang L, Mi F, Cao Y, Liu CL, Tang XZ, Wang PF, Xu JP (2021) Exploring the species diversity of edible mushrooms in Yunnan, southwestern China, by DNA barcoding. Journal of Fungi 7(4): e310. https://doi.org/10.3390/jof7040310